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COMPATIBILITY OF CERTAIN NICOTIANA SPECIES

F. A. McCRAY
Harvard University, Forest Hills, Massachusetts

Received April 11, 1932

INTRODUCTION

The genus Nicotiana has been the subject of many cytological and genetic investigations. Much yet remains to be done, however, before the phylogeny of this rather large group of species is well understood. At the outset of the work herein reported it was thought advisable, first, to extend the available information on the compatibility and relationships of the numerous species of the genus by making a number of crosses, especially some not previously attempted. The second problem undertaken has grown out of the first. In the course of the crossing together of different species a partially fertile triple species hybrid was produced (*rustica* var. *humilis* $\times$ *paniculata*) $\times$ *Langsdorffii*. A discussion of the cytological and genetic nature of these plants together with a brief discussion of their progeny, will be published as a separate paper. The third and last problem to be undertaken as a part of this study, while more distinct, is still concerned with a study of interspecific hybrids. Some hybrids are very vigorous and also fertile. Others are scarcely able to germinate, or, if they grow at all, they are always weak and unproductive. In the case of other crosses capsules are formed but no viable seeds are produced. Several questions may be raised about the development of hybrid embryos in these different categories. A third paper, also in preparation, will discuss this phase of the work.

The investigations were begun in the fall of 1927 but had to be discontinued from August 1928 until September 1930, when another leave of absence from his regular work made it possible for the writer to resume his studies. Nearly all the F_1 seed was produced and many hybrids grown in 1928, but several lots of the F_1 seed were not planted until October 1930. This lapse of two years, then, must be borne in mind in considering the viability of these hybrids, and will be referred to again in that connection.

MATERIALS AND METHODS

All the plants and seeds used in these investigations were obtained at Bussey Institution, HARVARD UNIVERSITY, where the work was done. Most of the species had been under observation there for several years

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and have been described in numerous papers. All the plants used were grown in a screened greenhouse, and the usual precautions taken to prevent accidental crossing. All the pollinations were made by hand except as otherwise noted.

Seeds were germinated in sterilized soil in the seed bench, and the seedlings allowed to grow there until large enough to transplant.

EXPERIMENTS AND RESULTS

All of the very considerable amount of work done on this subject from the time of KÖLREUTER and GAERTNER up to 1928 has been summed up and brought together in one comprehensive paper by EAST (1928). This publication gives the authority for all species used except one, *Cavanillesii*, Dun. A few other publications will be referred to later.

The work of the present writer on the genus began with a number of F_1 hybrids he obtained from Mr. M. CHRISTOFF. These were described by CHRISTOFF (1928), but had not been adequately tested for fertility. During the fall of 1927 and the following winter these plants of 11 hybrid combinations were selfed and backcrossed to both parents, the number of pollinations of each kind varying usually from 10 to 110, 25 to 50 being the more common number. All of these hybrids failed to produce any viable seed. They were as follows: *suaveolens*×*longiflora*, *suaveolens*×*glutinosa*, *paniculata*×*glutinosa*, *plumbaginifolia*×*Langsdorffii*, *nudicaulis*×*trigonophylla*, *paniculata*×*Sanderae*, *Bigelovii*×*Tabacum* var. *macrophylla*, *longiflora*×*alata*, *glutinosa*×*nudicaulis*, *suaveolens*×*plumbaginifolia*, and *plumbaginifolia*×*alata*.

My own crosses in some cases were a repetition of the work of others, but for the most part new combinations were tried. Altogether 195 combinations were made between 21 species. In a few cases some of these might be considered duplicates since more than one variety of *rustica* and *Tabacum* were crossed with the same species, not always with exactly the same result, however. These 21 species used, their gametic chromosome numbers, and a summary of results of the crosses made, are shown in table 1. The number of pollinations made in each case was from 1 to 14, probably averaging about 5.

As may be seen from the table, 15 of the 195 crosses made, marked (v), gave vigorous hybrids. These were as follows: *Langsdorffii*×*glauca*, *glauca*×*plumbaginifolia*, *paniculata*×*glauca*, *Palmeri*×*Rusbyi*, *Palmeri*×*tomentosa*, *trigonophylla*×*tomentosa*, *paniculata*×*rustica* var. *humilis*, *suaveolens*×*glauca*, *nudicaulis*×*glauca*, *nudicaulis*×*Palmeri*, *nudicaulis*×*Rusbyi*, *Bigelovii*×*glauca*, *Tabacum* var. *macrophylla*×*glutinosa*, *trigonophylla*

TABLE 1

Compatibility of species.

♀ \ ♂	CHROMOSOME NUMBER	*alata*	*Langsdorffii*	*Sanderae*	*longiflora*	*plumbaginifolia*	*acuminata*	*caudigera*	*Cavanillesii*	*glauca*	*glutinosa*	*Palmeri*	*paniculata*	*Rusbyi*	*sylvestris*	*tomentosa*	*trigonophylla*	*suaveolens*	*Bigelovii*	*nudicaulis*	*rustica* var. *humilis*	*rustica* var. *pumila*	*Tabacum angustifolia*	*Tabacum macrophylla*	*Tabacum purpurea*
CHROMOSOME NUMBER		9	9	9	10	10	12	12	12	12	12	12	12	12	12	12	12	16	24	24	24	24	24	24	24
alata	9	..	..	..	..	..	..	..	..	o	..	o	o	o	..	o	..	..	..	..	..	..	..	..	..
Langsdorffii	9	s	..	..	..	..	..	o	..	v♯	..	o	..	o	..	o	..	..	..	o	o	..	..	..	..
Sanderae	9	..	..	..	..	..	..	o	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
longiflora	10	..	..	..	..	s	..	o	..	o	..	o	..	o	o	o	..	..	..	..	..	..	..	..	..
plumbaginifolia	10	..	s	..	s	..	..	o	..	y	..	o	..	o	..	d	..	..	..	..	..	..	..	..	..
acuminata	12	o	..	..	..	..	..	..	..	o	..	o	o	d	..	d	..	..	..	..	..	..	..	..	..
caudigera	12	o	o	o	o	o	s	..	o	o	o	o	o	o	o	..	o	o	o	..	o	..	..	o	o
Cavanillesii	12	..	..	..	..	..	o	o	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
glauca	12	d	..	..	o	v♯	d	o	..	..	o	o	o	o	o	d	o	o	o	o	o	..	..	o	..
glutinosa	12	..	o	..	..	..	..	o	..	y♯	..	o	o	w	y	y	..	..	..	..	o	..	..	..	..
Palmeri	12	d	d	..	d	d	d	..	..	d	d	..	d	v	d	v	d	d	..	d	d	..	..	d	..
paniculata	12	..	..	..	..	..	d	o	..	v	..	o	..	d	..	..	..	..	..	..	v	o	..	d	..
Rusbyi	12	d	d	..	o	d	o	..	..	o	o	o	o	..	o	o	..	o	o	..	o	..	..	d	..
sylvestris	12	..	..	..	o	..	..	o	..	o	d	o	..	..	..	..	..	..	..	..	..	..	..	..	..
tomentosa	12	d	o	..	d	d	o	..	..	d	o	o	o	..	o	o	o	o	o	..	d	..	..	o	..
trigonophylla	12	..	..	..	..	..	..	o	..	d	..	v	..	..	..	v	..	..	..	..	..	..	..	..	..
suaveolens	16	..	..	..	..	..	..	..	..	v	..	d	..	o	..	d	..	..	..	..	..	..	..	..	w
Bigelovii	24	..	..	..	..	..	..	o	..	v♯	..	o	..	d	..	w	..	..	..	..	..	..	..	..	..
nudicaulis	24	..	d	..	..	..	..	s	..	v♯	..	v	..	v	w	..	..	..	..	..	..	..	..	..	w
rustica, humilis	24	..	w	..	..	..	..	o	..	d, m	o	d	s	d	..	..	..	..	..	..	..	..	s	d	s
rustica, pumila	24	..	..	..	..	..	..	o	..	..	..	..	..	d, m	..	..	..	..	..	..	..	..	o	d, m	..
Tabacum, angustifolia	24	..	..	..	..	..	..	s	..	..	w	..	..	..	..	o	..	..	..	..	o	d, m	..	..	..
Tabacum, macrophylla	24	..	d	..	..	..	..	o	..	d, m	v	o	..	..	..	v	..	..	..	..	o	o	..	..	..
Tabacum, purpurea	24	..	d	..	..	..	..	d	..	..	d	..	..	..	..	d	..	..	..	..	o	o	..	..	..

Legend: v, vigorous hybrids; y, young hybrids; w, weak hybrids; s, seed not tested; d, dead seed; o, no stimulation; m, maternal plants; ♯ plants variable.

×*Palmeri*, and *Tabacum* var. *macrophylla*×*tomentosa*. Nine of these crosses are believed to be here reported for the first time, *Langsdorffii*× *glauca*, *glauca*×*plumbaginifolia*, *Palmeri*×*Rusbyi*, *Palmeri*×*tomentosa*, *suaveolens*×*glauca*, *nudicaulis*×*Palmeri*, *nudicaulis*×*Rusbyi*, *Bigelovii*× *glauca*, and *trigonophylla*×*Palmeri*.

Four other hybrid combinations, *plumbaginifolia*×*glauca*, *glutinosa*× *glauca*, *glutinosa*×*sylvestris*, and *glutinosa*×*tomentosa*, designated by (y), gave plants which seemed to be vigorous but which were discarded in an

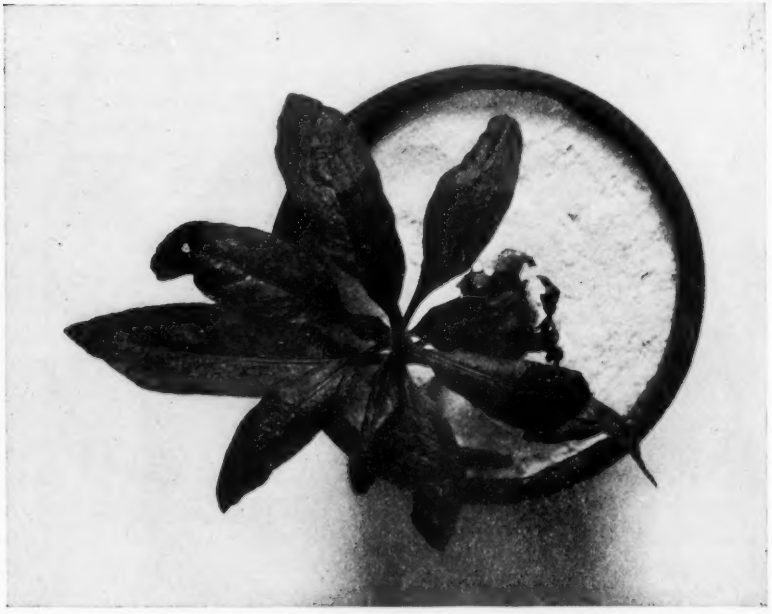

FIGURE 1.—Deformed plant, *Bigelovii*×*glauca*.

immature condition when the work was discontinued, and this point could not be exactly determined. They had, however, already definitely demonstrated their hybrid nature by certain paternal characters. The first and last of this group are new hybrids.

Some of these 19 hybrids will be described later but it is interesting to note here in passing that five of the group grown in 1928, *Langsdorffii*× *glauca*, *glauca*×*plumbaginifolia*, *Bigelovii*×*glauca*, *glutinosa*×*glauca* and *nudicaulis*×*glauca*, showed a very noticeable lack of uniformity among the

plants grown, of which there were usually five. Another lot of *Bigelovii*×*glauca* seed grown in 1931 showed again the same kind of variation. The differences involved practically all leaf characters and in some cases were quite striking. In *Bigelovii*×*glauca* some of the plants had numerous thick, rubbery, dark colored, curly, asymmetrical leaves growing close together. These plants made a very poor growth and had a dwarfed, distorted appearance. Such a plant is shown in figure 1. The growth indicated here was accomplished only after liberal applications of sodium nitrate. *Nicotiana glutinosa*×*glauca* and *nudicaulis*×*glauca* exhibited similar abnormalities in the texture and symmetry of the leaves. It is interesting to note further that each of these five hybrids had *glauca* as one parent. There appears to be nothing in our observations to explain the variability noted.

This group of 19 hybrids includes one pair of reciprocals, the crosses between *plumbaginifolia* and *glauca*.

Seven other combinations, indicated in the table by (w), produced hybrids which made only a weak growth, namely, *glutinosa*×*Rusbyi*, *Bigelovii*×*tomentosa*, *nudicaulis*×*sylvestris*, *rustica* var. *humilis*×*Langsdorffii*, *Tabacum* var. *angustifolia*×*glutinosa*, *nudicaulis*×*Tabacum* var. *purpurea*, and *suaveolens*×*Tabacum* var. *purpurea*. The first three of these also are believed not to have appeared in the literature before. The other four had already been produced by EAST, CHRISTOFF, and KOSTOFF (EAST 1928). The *Tabacum*×*glutinosa* cross has usually given vigorous plants, but my two year old seeds may have lost some of their vigor. It was at first thought that possibly some unfavorable environmental factor was stopping the growth of these seedlings, so more were transplanted as a check. Altogether 18 were tested and some given special care. Nevertheless all died at the same young seedling stage, except one. This one plant which made a normal growth, and which proved to be a haploid *Tabacum* with all the maternal characters, has already been described (MCCRAY 1932).

Eleven other combinations, marked (s) in the table, produced seed which has not been tested. In several cases data were already available from the work of other investigators, showing that hybrids are obtained from these crosses. This is not true, however, so far as I am aware, in the case of the seeds obtained from the cross *caudigera*×*acuminata*. The viability of this cross remains unknown, but from the similarity of the parents one might expect it would be successful.

Fifty-one other crosses, indicated by (d), produced some seed which, however, either failed to grow or was so evidently parthenocarpic that it was discarded. Five of these lots did give some plants but they were pure

maternals. In the 108 cases designated by (o) the flowers dropped before maturity.

Descriptions are available for the 11 new hybrids which made any considerable growth and will be given in the order in which they were originally named.

Langsdorffii×*glauca* plants made a tall vigorous growth. Three of them were viscid like *Langsdorffii* and had comparatively thick soft leaves. Two others were non-viscid, with a very short pubescence, and leaves much

FIGURE 2.—a, flower of *Palmeri*×*Rusbyi;* b, flower of *Palmeri.*

thinner and smoother than the others, resembling in these traits *glauca* somewhat more than *Langsdorffii.*

N. glauca×*plumbaginifolia* likewise produced vigorous plants showing marked variations. Three were slightly viscid with a fairly thick pubescence. Two others had little or none of either condition. In leaf form they resembled both parents. The leaves were rather broadly ovate with either acute or obtuse tips and bases, and were sessile with a narrow wing running down the midrib, showing clearly here the influence of the male parent. As in the preceding cross the plants differed considerably also in leaf texture. One had quite thick leaves, one very thin, while three were

intermediate in this respect. On one of these plants the leaves were rather bullate and rough to the touch. The flowers of this cross resembled the male parent somewhat more closely, being green in color and having the corolla limb sharply lobed. The length of the lobes, however, was only about 4 mm so the flower was narrow as in *glauca*.

The plants of *Palmeri*×*Rusbyi* are vigorous and have a long, fine, woolly pubescence, and large leaves, up to 7½ inches in length, pubescent on both

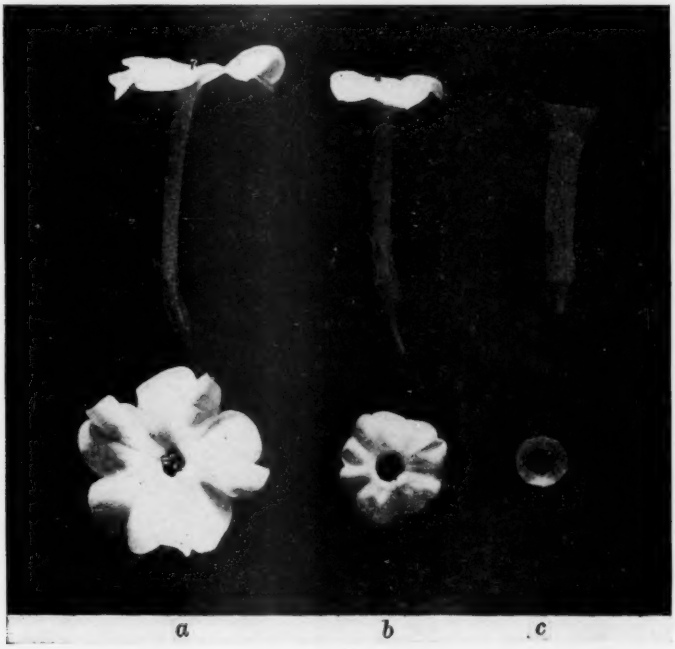

FIGURE 3.—a, flower of *suaveolens;* b, flower of *suaveolens*×*glauca;* c, flower of *glauca*.

sides. In these traits they stand somewhat closer to *Rusbyi*. In other leaf characters the parents are similar. The flowers of this cross are compared with those of *Palmeri* in figure 2.

The cross *Palmeri*×*tomentosa* closely resembles the last, as would be expected from the similarity of *Rusbyi* and *tomentosa*. Where the parents differ much in leaf and stem characters the hybrids resemble *tomentosa* somewhat more closely. They did not flower during the period of observation.

The plants of the cross *suaveolens*×*glauca* were like *suaveolens* in most leaf characters, but showed the *glauca* influence by having the base of the leaf reduced to a very narrow wing so the leaves were almost petiolate. The flowers of the hybrid and its parents are illustrated in figure 3.

Nicotiana nudicaulis×*Palmeri* produces hybrid offspring much more like *nudicaulis* than like *Palmeri*, but they resemble the latter in having somewhat lanceolate leaves and pointed lobes on the corolla limb, instead of rounding as in *nudicaulis*.

Nicotiana nudicaulis×*Rusbyi* is like *Rusbyi* in practically all vegetative characters, but is intermediate in flower size and color, and in the shape

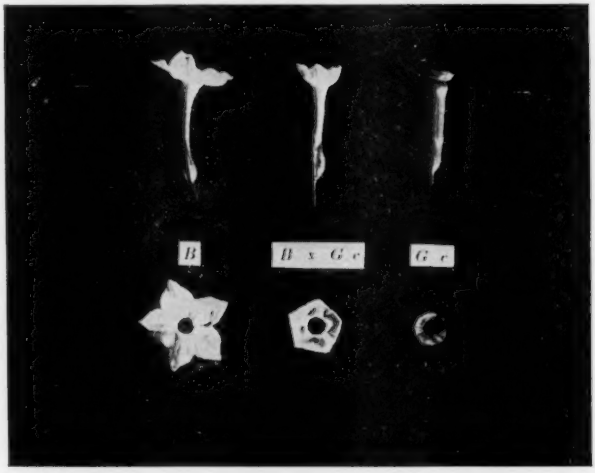

FIGURE 4.—B, flower of *Bigelovii;* B×Gc, flower of *Bigelovii*×*glauca;* Gc, flower of *glauca*.

of the corolla lobes. Two flowers averaged 12 mm across the corolla limb and 18 mm in length. Corresponding measurements for *nudicaulis* and *Rusbyi*, respectively, are 8×14 mm and 28.5×40 mm. The corolla tubes are green, more like *nudicaulis*, but the limb has a faint pink color from the *Rusbyi* parent. In pure *nudicaulis* the lobes of the corolla limb are rounded and shallow. In *Rusbyi* they are deeper and acute pointed. A combination of these traits makes the lobes in the hybrid shallow with acuminate tips.

A partial description of *Bigelovii*×*glauca* has already been given in noting some of the differences between the plants. The leaves were

smooth, more like *glauca*. The inflorescence also was more like that of *glauca*, each branch bearing a small panicle. The flowers were intermediate in length of corolla tube, and length, width, and shape of the limb, as shown in figure 4. In color, however, they were white like *Bigelovii*.

Nicotiana trigonophylla and *Palmeri* are so very similar that it was to be expected, as pointed out by EAST (1928), that they should cross easily and produce at least partially fertile hybrids. Such is the case. At least, each pollination made between them, crossing both ways, produced a good sized capsule of seed in 1928. When planted in 1930, the *Palmeri*×*trigonophylla* seed failed to germinate. One of the reciprocal hybrids, however, germinated, grew vigorously, and bore numerous capsules apparently full of seed, both from hand selfing and from natural selfing. This plant naturally resembled both parents closely. About the only distinctive difference between the parents is a larger flower size in *Palmeri*. This trait is also displayed by the hybrid.

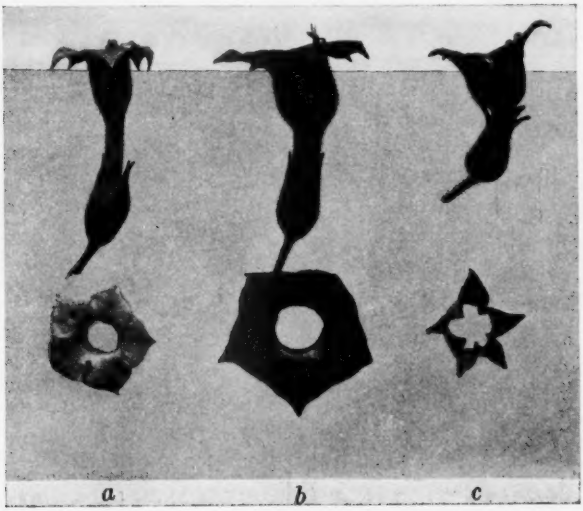

FIGURE 5.—a, flower of *Tabacum* var. *macrophylla;* b, flower of *Tabacum* var. *macrophylla*×*glutinosa;* c, flower of *glutinosa*.

Nicotiana plumbaginifolia×*glauca*, like *suaveolens*×*glauca*, showed the *glauca* influence by having the bases of its sessile leaves reduced to a very narrow wing, making the leaves almost petiolate. They seemed to be more upright in growth also than is *plumbaginifolia*.

Nicotiana glutinosa×*tomentosa* is also distinguished from its maternal parent by leaf shape. The latter has petiolate leaves with a cordate base, while the hybrid has sessile leaves like *tomentosa*.

Another hybrid which has been described before is pictured in figures 5 and 6, which show flowers and leaves of the cross *Tabacum* var. *macrophylla* ×*glutinosa*, and of its parents.

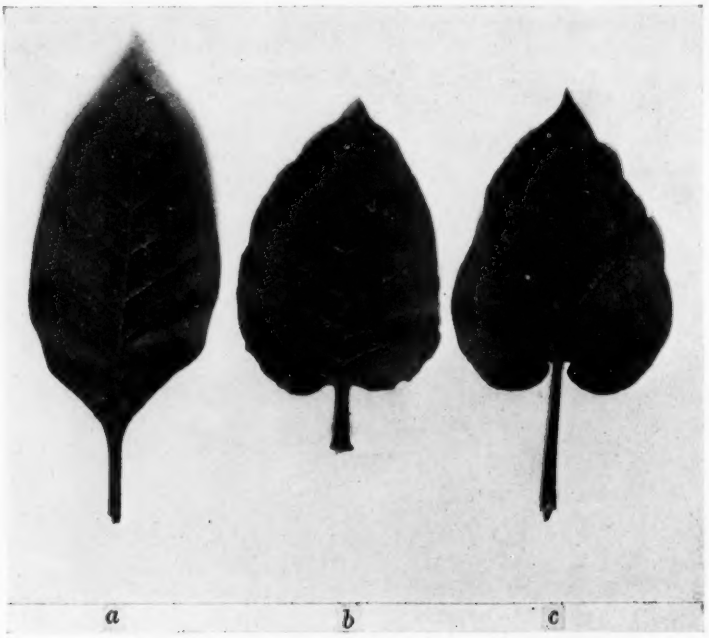

FIGURE 6.—a, leaf of *Tabacum* var. *macrophylla;* b, leaf of *Tabacum* var. *macrophylla*×*glutinosa;* c, leaf of *glutinosa*.

Only two of my hybrids, *nudicaulis*×*glauca* and *paniculata*×*glauca*, had matured when left in 1928, and as most of the hybrids produced that season did not grow again in 1930, the tests of fertility are very limited. The former of these two was pollinated only with *glauca* pollen, 4 times. Two capsules resulted, one of which was about ¼ full of seeds. They failed to germinate in 1930. *N. paniculata*×*glauca* was pollinated 16 times with *paniculata* pollen, 11 times with *glauca* pollen, and selfed once, but produced no capsules at all.

One *Bigelovii*×*glauca* plant was selfed once and backcrossed 11 times to the female parent and 3 times to the male. No capsules resulted.

The apparent fertility of *trigonophylla*×*Palmeri* has already been mentioned. The seeds produced by selfing have not yet been tested.

DISCUSSION

Where the crosses made here parallel other investigations, no important differences in the results were found. Quite likely some of the hybrid seed which failed to grow in 1930 might have grown in 1928. Out of 35 kinds of seed planted in October 1930, 12 which had grown before failed to germinate. Two others, *glutinosa*×*sylvestris* and *Tabacum* var. *angustifolia*×*glutinosa*, developed only into weak unsuccessful plants, whereas earlier tests have given vigorous hybrids in these cases. But at the same time so many of these F_1 seeds failed, in 5 cases out of the 35, maternals were produced in 1930 and these plants were vigorous and made a normal growth. This would seem to indicate that pure seed in these species retains its viability longer than hybrid seed.

It has been suggested (CHRISTOFF 1928) that in this genus the interspecific hybrids are easier to make if the species with the larger chromosome number is used as the female, and that (EAST 1928) the hybrid plants tend to resemble the species with the larger number of chromosomes. Some support is given the first claim by the data here presented. The two parallel lines in table one enclose crosses between species having 12 chromosomes each. Even a casual inspection of the table reveals the fact that most of the hybrids produced lie either in this rectangle or immediately below it, where the female parent has a larger chromosome number than the male. More explicitly, out of 23 hybrids produced, 11 had the higher chromosome species as the female parent. In 9 cases each species had 12 chromosomes, and in only 3 the male parent had the higher chromosome number. To look at the same problem in another way, in seven cases involving two different chromosome numbers the crosses were successful when the female had the larger chromosome number, but in only one case, *glauca*×*plumbaginifolia*, was the reciprocal, *plumbaginifolia*×*glauca*, obtained.

A more complete test of this hypothesis is secured by considering the 79 hybrids charted in EAST's table 2, together with my 14 new hybrids, which gives a total of 93 crosses between 22 species. The number of crosses entered into by each species is shown in table 2.

Twelve of these 22 species varying in chromosome number all the way from 9 to 24 showed about the same compatibility with other species

TABLE 2

Compatibility of certain Nicotiana species used as ♀ and as ♂.

SPECIES MORE OFTEN SUCCESSFUL AS ♀				SPECIES MORE OFTEN SUCCESSFUL AS ♂			
SPECIES	CHROMOSOME NUMBER	CROSSES AS ♀	CROSSES AS ♂	SPECIES	CHROMOSOME NUMBER	CROSSES AS ♀	CROSSES AS ♂
rustica	24	7	1	*Rusbyi*	12	3	6
glutinosa	12	8	4	*tomentosa*	12	3	9
paniculata	12	9	3	*Langsdorffii*	9	4	8
suaveolens	16	8	4	*sylvestris*	12	2	4
nudicaulis	24	7	2	*Sanderae*	9	2	7
Species about equally successful whether used as ♀ or as ♂.							
Tabacum	24	11	9	*Bigelovii*	24	6	7
glauca	12	7	10	*longiflora*	10	3	4
alata	9	5	7	*plumbaginifolia*	10	4	3
acuminata	12	0	1	*trigonophylla*	12	2	1
caudigera	12	0	0	*Palmeri*	12	2	2
Cavanillesii	12	0	0	*attenuata*	24	0	1

whether used as male or as female, and may therefore be left out of account. But not so with the other ten. Five of these species, *rustica*, *glutinosa*, *paniculata*, *suaveolens* and *nudicaulis*, succeed from 2 to 7 times as often in producing hybrids when used as the female as when used as the male. It will be noted that all of these species have from 12 to 24 chromosomes. Five other species, *Rusbyi*, *tomentosa*, *Langsdorffii*, *sylvestris* and *Sanderae*, succeed from 2 to 3 times as often as males as they do as females. And these have only from 9 to 12 chromosomes. In other words species with large chromosome numbers show somewhat more compatibility with other species when used as the female; and species with low chromosome numbers show somewhat more compatibility when used as males. Or, as CHRISTOFF suggests, crossing in Nicotiana is somewhat more likely to succeed when the species with the larger chromosome number is used as the female.

The evidence on the relation of chromosome number and resemblance of the hybrid to its parents is not so clear. Five of my crosses definitely resembled one of the parents more than the other. Three of these, *Bigelovii* × *glauca*, *nudicaulis* × *Palmeri*, and *nudicaulis* × *glauca*, appeared like the parent with the larger chromosome number, while the other two, *nudicaulis* × *Rusbyi*, and *Langsdorffii* × *glauca*, resembled more closely the species having the smaller chromosome number. But considering all the 93 crosses already mentioned, there are 22 which, in the opinion of the ob-

servers, resembled more closely the parent having the larger chromosome number; and only 3 which showed more resemblance to the parent with the lower chromosome number, *paniculata*×*alata* being the lone exception in addition to my two crosses just mentioned.

A third question might be raised, namely, how much correlation there is between the taxonomic relationship of the species and compatibility. I have tested the matter by classifying the 93 hybrids as shown in table 3, using for the purpose the taxonomic classifications followed by EAST, putting all the species into three groups, namely, *Tabacum*, *Rustica* and Petunioides. It should be noted here however that this writer questions the justification for the last two groups, and especially for Petunioides, and suggests that more complete information may warrant several subdivisions of the genus.

TABLE 3

Taxonomic relationship and compatibility of species.

NUMBER OF F_1 HYBRIDS SECURED BETWEEN SPECIES OF THE THREE GROUPS OF NICOTIANA

♀ \ ♂	*Tabacum*	*Rustica*	PETUNIOIDES	TOTAL
Tabacum	5	5	7	17
Rustica	8	9	18	35
Petunioides	11	12	18	41
Total	24	26	43	93

It will be seen from the table that there is little or no relationship between the present taxonomic standing of these species and their compatibility. The species of one group apparently cross about as freely with those of another group as with other members of their own group. And, in as much as many of these hybrids are the result of crossing very unlike species, it does not seem that the mere ability to produce hybrid progeny upon crossing would serve much better as a test of relationship of species in this genus. If a genetic basis of such classification were to be employed perhaps fertility of the hybrid would have to be used.

To summarize, the ability of Nicotiana species to produce F_1 hybrids seems to depend more upon the chromosome numbers involved than upon anything else; and the phenotype of the hybrid when produced usually is more like that of the parent having the higher chromosome number. Probably we may also conclude then that the resemblance of a hybrid to the parent species is not often determined by just a few dominant factors but rather by a relatively large number of factors scattered through the

chromosomes; and that, on the whole, the more chromosomes a species has the more likely is it that its hybrid progeny will exhibit its somatic characters.

Three species included in the investigation, namely, *Rusbyi*, *Palmeri* and *tomentosa*, have been used but little in earlier studies. It will be in order then to call special attention to their behavior in crossing with other species. *Rusbyi*, the hybrids of which with *Tabacum* have been made the subject of intensive study by BRIEGER (1928), was here crossed with 15 species as female, and with 14 as male. Only 3 hybrids resulted, *glutinosa* × *Rusbyi*, which was weak, and *Palmeri* × *Rusbyi* and *nudicaulis* × *Rusbyi*, which have already been described.

Nicotiana tomentosa, used in exactly the same number of crosses, and in most instances with the same species, produced 5 hybrids, and, as in the case of *Rusbyi*, always when it was used as the pollen parent. *Palmeri* × *tomentosa*, *trigonophylla* × *tomentosa*, and *Tabacum* var. *macrophylla* × *tomentosa* were vigorous plants, *Bigelovii* × *tomentosa* weak, and *glutinosa* × *tomentosa* apparently vigorous, but they did not mature during the period of observation.

Palmeri succeeded twice as female and twice as male in producing hybrids, which were vigorous in each case. Altogether the pollen of 16 species was used upon it, and its pollen was used on 18 other species. The 4 hybrids, *Palmeri* × *tomentosa*, *Palmeri* × *Rusbyi*, *nudicaulis* × *Palmeri*, and *trigonophylla* × *Palmeri*, have already been described.

The last combination is interesting because of the interfertility of these species. *Palmeri* and *trigonophylla* are so nearly alike in all somatic characters except flower size that they would defy differentiation; and a high degree of compatibility, if not fertility, was to be expected. If one may judge from the behavior of the single plant, the strains of these species used seem to breed together as freely as varieties, resembling, in this respect, *longiflora* and *plumbaginifolia* (EAST 1928, and other papers).

SUMMARY

1. The compatibility of 21 Nicotiana species is reported, 195 different combinations between them having been tried, many of them hitherto unattempted.

2. Fourteen new hybrids are listed, namely, *Langsdorffii* × *glauca*, *glauca* × *plumbaginifolia*, *Palmeri* × *Rusbyi*, *Palmeri* × *tomentosa*, *suaveolens* × *glauca*, *nudicaulis* × *Palmeri*, *nudicaulis* × *Rusbyi*, *Bigelovii* × *glauca*, *trigonophylla* × *Palmeri*, *plumbaginifolia* × *glauca*, *glutinosa* × *tomentosa*, *glutinosa* × *Rusbyi*, *Bigelovii* × *tomentosa*, and *nudicaulis* × *sylvestris*. Of these

the first 9 at least and probably 11 are vigorous in growth. The last three are weak. The first 11 are described, although not fully in all cases as some of them were immature when studied.

3. Supporting earlier observations, it seems that crosses are more likely to be successful if the species with the larger chromosome number is used as the female. There were seven cases in which two species with different chromosome numbers were crossed both ways, and in which the cross was successful when the female had the larger chromosome number. Only one of the reciprocal crosses produced a hybrid, *plumbaginifolia*×*glauca*. Out of 23 hybrids reported, 9 were produced by crossing a species of smaller chromosome number on a species with a larger chromosome number. Only 3 crosses were of the opposite type. In the 11 other cases the two species had the same chromosome number.

Evidence secured from a study of 79 other hybrids included in EAST's summary also shows a strong tendency for species in this genus to enter into interspecific crosses more readily when the species having the larger chromosome number is used as the female. Five of the 22 species involved in the combined list of 93 different hybrids having 12 to 24 chromosomes made many more hybrids when used as females; and 5 others having only 9 to 12 chromosomes produced many more hybrids when used as males.

4. The suggestion that the hybrids between these species more often bear a close resemblance to the parent having the higher chromosome number than to the other parent is also supported. The matter could be tested in only 5 hybrids among those produced by the writer, but including again the 79 others recorded by EAST, 22 of the combined group of 93, according to the observers, looked more like the parent with the larger number of chromosomes, and only 3 looked more like the other parent.

5. When these 93 hybrids were classified in a frequency table according to the taxonomic position of the parent species, no correlation could be detected between taxonomic relationship and ability to cross with other species. Inter-group crosses are about as numerous as crosses between species within a group.

6. Among the 21 species tested are 3 which have been used but little in earlier studies of compatibility, *Rusbyi*, *tomentosa*, and *Palmeri*. *Rusbyi* was crossed with 15 species as female and with 14 as male. Only 3 hybrids resulted, *glutinosa*×*Rusbyi*, which was weak, and *nudicaulis*×*Rusbyi* and *Palmeri*×*Rusbyi*, both of which were vigorous. *Nicotiana tomentosa*, used in the same number of crosses, produced 5 hybrids, always when used as male, *Palmeri*×*tomentosa*, *trigonophylla*×*tomentosa*, *Tabacum* var. *macrophylla*×*tomentosa*, and *glutinosa*×*tomentosa*, which were strong, and *Bige-*

lovii×*tomentosa* which was weak. *Palmeri* succeeded in producing 4 crosses, 2 when used as female and 2 when used as male. All of these hybrids, *Palmeri*×*tomentosa*, *Palmeri*×*Rusbyi*, *nudicaulis*×*Palmeri*, and *trigonophylla*×*Palmeri*, were vigorous. It was used 16 times as female and 18 times as male.

7. The species entering into the most crosses are *Tabacum*, *glauca* and *Bigelovii*, which accounted for 20, 17 and 13 respectively of the total of 93 crosses. Six other species, *glutinosa*, *paniculata*, *suaveolens*, *tomentosa*, *Langsdorffii* and *alata* participated in 12 crosses each.

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GENETIC AND CYTOLOGICAL STUDIES ON X-RADIATION INDUCED DOMINANT EYE COLORS OF DROSOPHILA[1]

E. A. VAN ATTA

Washington University, St. Louis, Missouri

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TABLE OF CONTENTS

	PAGE
INTRODUCTION	637
Method of obtaining mutations	638
Description of eye colors	639
Linkage groups	640
Methods of crossover tests	641
Genetic results	642
Allelomorphism of the dilute eye colors	647
Cytological analysis	648
DISCUSSION	655
SUMMARY	657
LITERATURE CITED	658

INTRODUCTION

Before 1927, when X-rays first came into use as a genetic tool, no mutations dominant to the normal red eye color were known in Drosophila. (Pale-translocation [BRIDGES 1923] diluted the eye color of flies homozygous for eosin.) WEINSTEIN (1928) was first to report a dominant eye color mutation resulting from X-ray irradiation. Descriptions are given by MULLER (1930) of several cases obtained by him and his associates. HANSON and WINKLEMAN (1929) found a dominant eye-color mutation, cream-eye, among the offspring of Drosophila exposed to radium irradiation. All the eye colors mentioned involve some sort of chromosome rearrangement, inversion or translocation, which is lethal in homozygous condition or occasionally produces abnormal homozygous individuals. The eye color is generally non-homogeneous, and considerable variation in the number of affected ommatidia is observed in the eyes of the offspring from a single mutated individual.

[1] The detailed tables used in the preparation of this article are on file at the BROOKLYN BOTANIC GARDEN and may be obtained for examination on request.

The experimental work has been made possible by the use of apparatus from the Committee on Effects of Radiation, NATIONAL RESEARCH COUNCIL, for which the author wishes to express appreciation.

The present investigation began in the fall of 1930 with the desire to obtain additional dominant mutations and to subject them to genetic and cytological examination in order to determine the possible relationships between the chromosomal abnormality and the expression of the dominant mutation.

The work was carried out under the direction of Doctor C. P. OLIVER to whom the writer is indebted for many helpful suggestions.

METHOD OF OBTAINING MUTATIONS

Normal adult males, placed in gelatine capsules, were given an X-ray treatment of approximately 4000 r units, calculated from ionization readings taken with a Victoreen dosimeter at the time of the exposure. The particular X-ray machine used gives this dosage under the following conditions: 52 kilovolts (peak), 5 milliamperes, distance of 20 cm from a tungsten target, aluminum filter of 1 mm thickness, and exposure time of 2.5 hours.

TABLE 1

Summary of the results of the X-ray experiments.

EXPERIMENT	PAIRS P_1	F_1 MALES	F_1 FEMALES	MUTATIONS FOUND	
				SEX-LINKED RECESSIVE	DOMINANT
1	675	1989	2566	13	27
2	1200	4929	6013	14	38
3	660	2560	2872	6	28
Total	2535	9478	11451	33	93

TABLE 2

Details of the occurrence of the dominant eye-color mutations.

NAME	SEX OF F_1	NUMBER OF EXPERIMENT AND BROOD	NUMBER OF CULTURE
Salmon	Female	I, 1	34
Henna	Male	II, 1	73
Dilute-2	Male	II, 2	1
Dilute-3	Female	III, 1	28
Dilute-4	Female	II, 2	53
Dilute-5	Male	II, 2	6
Dilute-6	Female	III, 1	12

The treated males were mated to untreated virgin females of the attached-X double-yellow race, and both male and female offspring were

examined for any visible departures from the normal type. Table 1 summarizes the results and table 2 gives the details of the occurrence of the seven dominant eye-color mutations to which this report is confined.

The F_1 males from the above mating inherit the treated X chromosome, and the F_1 females the treated Y chromosome. Both receive a treated second, third, and fourth chromosome. Therefore, the females show only autosomal dominant mutations and chromosomal aberrations involving the autosomes or the autosomes and the Y chromosome. The males may show autosomal dominants, sex-linked dominant or recessive mutations, and aberrations involving the autosomes or the autosomes and the X chromosome.

DESCRIPTION OF EYE COLORS

The seven dominant eye colors can be divided into two groups, the homogeneous and the non-homogeneous, with salmon and henna belonging in the former. Salmon-eye, a pinkish-red, differs only slightly from the normal color but is easily distinguished from it. In young flies the eye has a light purplish tinge which gradually changes to the characteristic deep salmon-pink of the adult.

Henna derives its name from the brownish-red appearance of the eye. Considerable variation occurs among different individuals and separation from the normal red is sometimes difficult. The color deepens slightly with age. In henna flies the body and wings appear somewhat broader than those of wild-type flies and the wings are more rounded at the distal ends.

The five non-homogeneous eye colors show a dilution of the red color in some of the ommatidia. Cream-eye, previously referred to, likewise appears dilute-red when vermilion is not present, and is included in this investigation, designated as dilute-1 (E. W. and L. C. Van Atta 1931). In dilute-1 and dilute-2 the effect is most pronounced. Usually all the ommatidia are mutated and the eye has a uniformly diluted red color. Usually in the dilute-3 eye are found large affected areas that contrast distinctly with the normal red color of the rest of the eye; however, in exceptional cases, either all the ommatidia or only a few are mutated. Dilute-4, dilute-5, and dilute-6 show the least variation from the normal. Usually only a few isolated cells of the eye are diluted, and these appear as dark spots against the red background, probably because the dark pigment at the base of the surrounding cells is visible through the mutated ommatidium. The ground color of the eye in these three mutations appears slightly duller than the normal red and the dark mutated ommatidia are best distinguished in young flies before age has darkened the ground color.

LINKAGE GROUPS

In order to study the linkage groups associated with the mutations, males or females with the dominant eye color were mated to individuals with the markers star, curly, and dichaete. The F_1 curly dichaete males with the dominant eye character were out-crossed to normal females. If a translocation is present the involved chromosomes (sex, II, III) behave as if completely linked due to the inviability (as a general rule) of the hyperploid and hypoploid classes. The distribution of the markers with reference to the dominant eye mutation then indicates the nature of the translocation. Table 3 gives the results of the tests. In table 4 are found the results of tests for the fourth chromosome as determined from back-crosses of males, heterozygous for eyeless and the dominant mutation, to homozygous eyeless females. In both tables *M* refers to the eye-color mutation.

TABLE 3

Results from out-crosses of Curly Dichaete mutant males.

NAME	CLASSES							LINKAGE GROUPS INVOLVED
	$+MC_yD$	MD	C_y	C_yD	M	MC_y	D	
Salmon		..	..	40	40			II-III
Henna		..	..	55	66			II-III
Dilute-1		209	230	220	232			II
Dilute-2		28	48	39	31			II
Dilute-3		35	36	52	43			II
Dilute-4		..	..	48	49			II-III
Dilute-5		..	..	47	54			II-III
Dilute-6		..	53*	82	92			II-III

* Surviving hyperploid individuals.

TABLE 4

Results from backcrosses of heterozygous mutant eyeless males.

NAME	CLASSES			
	M	e_y	Me_y	+
Salmon	29	17	27	18
Henna	24	30	14	17
Dilute-1	37	42	44	52
Dilute-2	31	31	30	33
Dilute-3	24	25	25	23
Dilute-4	32	31	35	30
Dilute-5	28	24	29	33
Dilute-6	27	50	..	..

It is evident that Salmon, Henna, Dilute-4, and Dilute-5 involve translocations between the second and third chromosomes; Dilute-6 includes the second, third, and fourth. The other mutations are located on the second chromosome. None survive in homozygous condition.

METHODS OF CROSSOVER TESTS

Dilute-1, Dilute-2, or Dilute-3 virgin females were mated to Curly males heterozygous for the "apl" combination containing the second-chromosome recessive genes aristaless (a_l), dumpy (d_y), black (b), purple (p_r), curved (c), plexus (p_z), and speck (s_p). F_1 virgin females with the dominant eye color and heterozygous for "apl" were backcrossed to homozygous "apl" males.

In the cases in which the eye color is associated with a translocation (Salmon, Henna, Dilute-4, Dilute-5, Dilute-6) the character Minute (M_{cIIIz}) was introduced into the matings. Minute is a dominant marker for the third chromosome, associated with an inversion which prevents crossing over. It accomplishes the twofold purpose of keeping the translocation and dominant eye color together if the latter is on the third chromosome, and revealing possible separations of the translocation and the mutation if the latter is on the second. Since the earlier experiments with Salmon, Dilute-4, and Dilute-5 indicated that the mutation and the translocation never separated, the later experiments were, for the sake of convenience, conducted without the Minute character. No significant differences in crossing over were noted in the results of the two series.

In order to investigate crossing over in the third chromosome, virgin females with the dominant eye color (Salmon, Henna, Dilute-4, Dilute-5, or Dilute-6) were mated to males heterozygous for Curly, Dichaete, and the "rucuPr" combination containing the third-chromosome recessive genes roughoid (r_u), hairy (h), thread (t_h), scarlet (s_t), curled (c_u), striped (s_r), sooty (e_s), and the dominant, Prickly bristles (P_r), located at a point about 15 units from the right end of the chromosome (MULLER 1930). Curly F_1 virgin females, with the dominant eye color and heterozygous for "rucuPr," were mated to males from the balanced stock Moiré "rucuca." The "rucuca" combination, containing claret instead of Prickly, is used due to the fact that Prickly in "rucuPr" is ordinarily lethal when homozygous. Only the non-Moiré offspring can be used for crossover counts.

Control crossover experiments for both the second and the third chromosomes were made at the same time and under identical conditions.

GENETIC RESULTS

In tables 5 and 6 are listed the crossover percentages for the second and third chromosomes and the number of flies examined. The results obtained from the control experiments are also included.

TABLE 5

Percentage of crossing over in the second chromosome.

	TOTAL NUMBER OF FLIES	a_l-d_y	d_y-b	b-p_r	p_r-c	c-p_x	p_x-a_p
Control	5754	11.7	28.1	6.0	18.4	23.5	4.4
					p_r-S_a S_a-c		
Salmon	3437	10.8	22.3	1.8	0.03 18.8	21.2	4.0
Dilute-1	2672	..	..	0.5	0.29	0.28	..
Dilute-2	3231	..	..	0.4	0.8	0.8	..
Dilute-3	5950	11.8	32.0	7.6	0.6	0.1	0.02
Dilute-4	2441	..	..	..	0.8	0.7	0.1
Dilute-5	2329	13.3	34.6	13.3	4.7	..	..
Dilute-6	917	..	..	..	..	..	..

TABLE 6

Percentage of crossing over in the third chromosome.

	TOTAL NUMBER OF FLIES	r_u-h	h-l_h	l_h-a_l	a_l-c_u	c_u-a_r	a_r-e_s	e_s-P_r
Control	1165	24.6	17.0	0.7	3.4	11.9	9.1	18.2
					s_r-S_a S_a-c_u			
Salmon	1345	27.3	17.0	0.3	2.5 3.2	15.4	10.7	19.5
Henna (without		r_u-H H_n-h						
translocation)	1345	23.4 3.5	22.5	0.4	.. 4.5	11.8	9.7	18.4
Henna (with trans-					s_r-* *-c_u			
location)	714	27.6 2.0	15.8	0.0	2.7 1.7	6.7	1.0	0.8
Dilute-4	1402	30.8	28.0	0.4	.. 4.3	0.1	0.1	0.1
Dilute-5	808	30.7	33.7	0.7	13.6 0.1	1.6	0.4	1.5
Dilute-6	791	26.0	17.3	0.0	0.03 2.2	9.7	10.1	20.3

Note: The symbol * is used to denote the point of breakage or attachment. Results for Henna are included only to show that the eye color is independent of the aberration.

Crossing over occurs with normal frequency in the right arm of the second chromosome of Salmon. In all parts of the left arm, crossing over is slightly decreased. The crossover classes indicate that the region of the chromosome involved in the translocation is between purple and curved, at or near the locus of purple. (The 0.03 percent is based on the appearance of a single curved-plexus-speck fly.) Since the locus of purple is known to

be to the left of the point of attachment of the spindle fiber (DOBZHANSKY 1930b), the break in the chromosome also must have occurred to the left of the spindle fiber. This is shown further by the reduction in crossing over in the left arm of the chromosome; according to DOBZHANSKY'S view a reduction in crossing over is generally found in the arm of the chromosome involved in the translocation. The third chromosome appears to be broken half-way between scarlet and curled, at or very near the point of spindle-fiber attachment, which is also about half-way between the two genes (DOBZHANSKY 1930a). Crossing over appears normal or even slightly increased in both arms of the chromosome. It is not clear which fragment retains the spindle fiber; however, the crossover percentages favor the right arm. Since the break in each chromosome occurs near the locus of the spindle-fiber attachment and crossing over remains practically normal in every region of both chromosomes, Salmon translocation must consist of a mutual interchange of parts. The left arm of the second chromosome and the left or right arm (probably the left) of the third were broken; the detached pieces exchanged places; and each fragment became reattached by its broken end to the point of breakage on the non-homologous chromosome. Apparently the dominant eye-color gene is located exactly at the point of breakage of one of the chromosomes, since the mutation never separates from the translocation even though crossing over occurs with a normal frequency in all regions of both involved chromosomes.

Henna, found to be located between roughoid and hairy, behaves as if it were due to a definite point mutation independent of the chromosomal aberration. When the translocation is not present, crossing over apparently occurs with a normal frequency through almost the entire extent of the third chromosome; it is quite probable that the slight increase in the hairy-thread region is, under the conditions, without significance. With the translocation present, crossing over is decreased in the right arm and the distribution of Curly and non-Curly classes indicates that a locus of the third chromosome between scarlet and curled is involved in the aberration. Crossover percentages for the second chromosome of the translocation also show considerable reduction in crossing over in the right arm. However, the numbers are insufficient in both second and third chromosome tests, and at present it is impossible to state the exact nature of the aberration.

All the flies heterozygous for the Henna translocation and containing the "apl" combination in the other second chromosome showed an extreme form of the dumpy character, indicating either a mutation to dumpy (referred to as dumpy-2) or the loss of a small fragment. Very few individuals

emerged and their viability was poor. Females backcrossed to homozygous "apl" males gave crossing over between aristaless and dumpy-2 and between dumpy-2 and black. None occurred between the original dumpy and dumpy-2. Since the crossover percentages, in spite of the small numbers, agree very well with the normal values for crossing over around the original dumpy, it may be concluded that dumpy-2 is an allelomorph of the original dumpy that occurred simultaneously with the dominant eye-color mutation and the translocation.

Of the three non-homogeneous eye colors (Dilute-1, Dilute-2, and Dilute -3) involving only the second chromosome, Dilute-1 and Dilute-2 are apparently associated with the same type of chromosomal rearrangement. The crossovers listed in table 7 are practically identical, although crossing over occurs with significantly greater frequency in Dilute-1.

TABLE 7

Crossover classes for Dilute-1 and Dilute-2.

CLASSES	DILUTE-1	DILUTE-2
Non-crossovers	2531	3190
Crossovers		
$a_l\ d_y\ b\ D_l$ and $p_r\ c\ p_z\ s_p$	12	12
$c\ p_z\ s_p$	4	..
$a_l\ d_y\ b\ p_r\ c\ D_l$	1	..
$a_l\ d_y\ b\ p_r\ p_z\ s_p$ and $c\ D_l$	79	29

From the results it is probable that the left arm of the chromosome, including the locus of black, has become attached by its terminal end to the end of the right arm. This condition can explain the frequent occurrence of double crossovers in the right arm ($a_l\ d_y\ b\ p_r\ p_z\ s_p$ and $c\ D_l$) and also account for the absence of single crossovers in the left and right arms. It is here assumed that homologous parts with the same gene arrangements can more readily pair with each other. Accordingly, the other crossovers involving the b-p_r, p_r-c, and c-p_z regions must also involve crossing over between speck and the point of attachment of the fragment from the left end of the chromosome (hence, double crossovers). It appears also that the Dilute-1 mutation (and probably Dilute-2) is located in the right arm of the second chromosome somewhere in the plexus-speck region, since, in one fly, a double crossover ($a_l,\ d_y\ b\ p_r\ c\ D_l$), plexus and speck are replaced by the homologous section containing Dilute-1.

In Dilute-3, associated with another type of second-chromosome aberration, crossing over occurs in the left arm with a frequency at least as

great as (probably greater than) that in the controls. The absence of single crossovers in the right arm, with the exception of a few between purple and curved, indicates the occurrence of an inversion. The dominant eye-color mutation appears to be located in the inverted region.

The other Dilute eye colors (Dilute-4, Dilute-5, and Dilute-6) are connected with aberrations that involve the second and third chromosomes and, with Dilute-6, the fourth as well. Crossing over in Dilute-4 is limited in the second chromosome to a few crossovers in the right arm (1 *a*$_l$ *d*$_y$ *b* *p*$_r$ *D*$_l$, 2 *a*$_l$ *d*$_y$ *b* *p*$_r$ *p*$_z$ *s*$_p$, 14 *c* *D*$_l$, and 2 *c* *p*$_z$ *D*$_l$, or 18 crossovers in 2441 flies). Obviously, the second chromosome has undergone a radical rearrangement. On the other hand, crossing over in the left arm of the third chromosome is slightly greater than normal but that in the right arm is considerably reduced below the expected amounts. It is impossible from these data to determine the exact nature of the translocation.

Crossing over in the second chromosome of Dilute-5 is above the normal frequency in the left arm, greatly reduced in the purple-curved region, and entirely prevented in the region from curved to the end of the right arm. According to the crossover classes, the region involved in the translocation must be to the right of curved. In the third chromosome there is also a reduction of crossing over in the right arm, and the crossover classes show the locus of the break is between scarlet and curled. The results for both chromosomes point to the conclusion that the right arm of the third chromosome is broken between scarlet and curled and that the fiberless fragment is attached to the right arm of the second chromosome.

The appearance of Curly hyperploid individuals among the offspring of the out-crossed Curly Dichaete Dilute-6 males (table 3) indicates that at least one small translocation must be present. A further test, made by mating Star Curly Dichaete homozygous eyeless females to Dilute-6 males and backcrossing the Star Dichaete Dilute-6 F_1 males heterozygous for eyeless to homozygous eyeless females, produced in the F_2 generation the expected classes of 37 Dilute-6, 35 Star Dichaete eyeless, and the unexpected classes of 20 Star eyeless and 3 Dichaete Dilute-6. The three flies of the last named class have a number of characters usually observed in Minute flies, especially the small bristles. An interpretation of the results may be that one fragment of the second chromosome is translocated to the third chromosome, and another (also fiberless) fragment of the second chromosome is translocated to the fourth chromosome. The Star eyeless flies are hyperploid for the fragment of the second chromosome that is attached to the third chromosome, and the three Dilute-6 Dichaete

(Minute) flies are hypoploid for the same piece. That this is the correct explanation is also shown by the offspring of the next mating.

When Dilute-6 females were mated to Curly Minute-c_{IIIX} males heterozygous for "apl," two exceptional types of F_1 flies appeared. Several individuals, that were non-Curly, non-Minute, and non-Dilute-6 showed the two recessive characters, purple and speck. These flies were sterile. A few Dilute-6 flies, with the Minute character, were also extreme plexus. The former can be explained only by assuming them to be hypoploid individuals lacking two small pieces of the second chromosome (instead of one) that are attached to the fourth chromosome. They must have the second chromosome of the aberration for they show the recessive characters and they must also have the third chromosome involved in the translocation, because, as shown above, when hypoploid for the piece attached to the third, the Minute character shows. The latter must be hypoploid for the piece of the second attached to the third chromosome.

When Dilute-6 Minute-c_{IIIX} virgin females, heterozygous for "apl," were backcrossed to homozygous "apl" males, probably no actual crossover classes appeared among the offspring. However, some unexpected classes did appear.

TABLE 8

Crossover classes for Dilute-6.

CLASSES	NUMBER
Expected	
Dilute-6	661
$a_l\ d_y\ b\ p_r\ c\ p_z\ s_p\ M_{cIII_z}$	88
Unexpected	
$a_l\ d_y\ b\ p_r\ c\ s_p$	517
Dilute-6 $p_z\ M_{cIII_z}$	34
$a_l\ d_y\ b\ c$	117

Our conclusions being based upon the hyperploid and hypoploid individuals observed in the matings mentioned earlier, the $a_l\ d_y\ b\ p_r\ c\ s_p$ individuals from this mating, which were non-Minute and non-Dilute-6, were therefore hyperploid for the fragment of the second chromosome attached to the third, with plexus suppressed by its normal allelomorph carried in the translocated fragment. The Dilute-6 plexus Minute-c_{IIIX} flies are hypoploid for the same fragment. The $a_l\ d_y\ b\ c$ offspring may be explained as doubly hyperploid, containing, besides both chromosomes of the "apl" combination, the fragment of the second chromosome attached

to the third and covering plexus, and the two fragments attached to the fourth chromosome, covering purple and speck.

In one exceptional fly that appeared among the offspring of the "apl" backcross, both eyes showed the Dilute-6 character but only one side of the thorax was Minute and only the wing on that side was extreme plexus. The bristles on both sides of the head did not show the Minute character. A possible explanation is that the small fragment attached to the third chromosome was lost in an early embryonic cell. This is known from evidence given above to permit the uncovered plexus to appear and also to tend to cause the Minute trait. In other tests with Dilute-6, flies occasionally appeared in which one side of the thorax was Minute.

Crossover classes for the third chromosome, based on small numbers, show that the fragment of the second is attached to the third chromosome at a locus near scarlet. Crossing over is somewhat reduced on either side of the scarlet-curled region but occurs with normal frequency everywhere else. In all the matings, the distribution of the Dilute-6 eye color with respect to the involved chromosomes indicates strongly that the condition responsible for the mutation is located in one of the parts of the second chromosome attached to the fourth.

ALLELOMORPHISM OF THE DILUTE EYE COLORS

Results with the non-homogeneous eye colors show that in every case there is some sort of chromosomal rearrangement, involving the right end of the second chromosome, that cannot be separated from the mutation. Accordingly the possibility that all the Dilute eye colors might be due to mutations in this region was tested by matings in which a counterbalanced stock of BRIDGES' Pale-translocation was used. Virgin females of this stock were mated to heterozygous Star Dichaete Dilute males and the F_1 Curly Delta Hairless individuals (hyperploid for the translocated piece of Pale) were examined. If the dominant eye color is due to a mutation in a part of the second chromosome that is covered by the translocated piece, its expression may be altered or suppressed by the presence of the two normal allelomorphs, one in the Curly-bearing chromosome and the other in the translocated piece of the second chromosome. REDFIELD (1930) finds that some dominants in the presence of two normal allelomorphs may not have an observable effect.

Each of the Dilute eye colors was tested with Pale, and an examination of the F_1 hyperploid individuals showed that in each case the Dilute eye color was entirely suppressed. The eye colors therefore are all located in the right arm of the second chromosome somewhere in the region from the

left of plexus to the end of the chromosome. Tests showed, however, that this was not true for Salmon and Henna.

The question then arises: Do the Dilute eye colors form an allelomorphic series? Two recessive lethal mutations in homologous chromosomes will not exert a lethal effect unless they are at the same locus, that is, allelomorphic to each other. Since the Dilute eye color mutations all have a recessive lethal effect, it should be possible, using this criterion, to establish their allelomorphism. Accordingly Curly Dilute-1 females were mated to Curly Dilute-2 males. The F_1 offspring should be Curly Dilute-1, Curly Dilute-2, and Dilute-1 Dilute-2 in equal numbers. If the third class does not appear, it may be said that this is due to the lethal action of two mutations at the same locus. This type of mating was repeated with all possible combinations of the Dilute eye colors and the results in every case showed no surviving Dilute-Dilute offspring. From this evidence we conclude that the Dilute eye colors represent a series of multiple allelomorphs, the locus involved being in the plexus-speck region of the second chromosome, probably to the right of plexus.

CYTOLOGICAL ANALYSIS

Oögonial cells were obtained from females less than twenty-four hours old. The ovaries were dissected out in physiological salt solution and fixed for three hours in a fresh solution of the following fluid:

95 percent alcohol	25 cc
Glacial acetic	2
Com. formalin	4
Water	20

The fixed tissue is colorless but if stained in bulk with eosin it is easily visible during embedding and sectioning. Sections were cut five micra in thickness and stained with Haidenhain's iron-alum haematoxylin. The slides were examined with a Spencer binocular microscope using a 97× oil immersion objective of 1.25 N.A. Conclusions were drawn from usually more than six clear cells of each mutant type.

In spite of the familiarity of the typical chromosome configuration of *Drosophila melanogaster*, several of its characteristics are here reviewed briefly for the purpose of comparing the normal type with the conditions observed in the chromosomal aberrations. Figure 1 shows the four pairs of chromosomes in their characteristic positions in a normal chromosome configuration. The two rod-shaped X chromosomes, usually designated as the first pair, lie close together at one side of the cell, with their narrower

ends, the regions of spindle-fiber attachment, directed toward the center. The fourth chromosomes are small and round, closely paired, and central in position. The large autosomes (that is, the second and third pairs) are V shaped, narrow in the middle and wide, rather knob like, at the ends. They orient themselves in such a way that the angle, which is the locus of spindle-fiber attachment, turns toward the center of the cell; generally the two members of each pair lie close together with corresponding parts paired. The same orientation of the chromosomes is seen in figure 14 from a female containing the Henna mutation without the translocation.

The chromosome plates used for the investigations of the dominant eye colors were obtained from females that were abnormal only for the eye color and the connected chromosomal aberration. Each plate contains two X chromosomes that lie in the usual position with the more pointed ends directed toward the center of the cell. Occasional foreshortening causes an apparent variation from the normal shape and size. In some instances there is very close pairing, with the chromosomes overlapping at the distal ends. The fourth chromosomes are paired and lie in their usual central position. The exceptions to this, found in figures 19 and 20, will be considered later.

It has already been pointed out that normal homologous chromosomes of Drosophila tend to lie close together at the metaphase stage of the oögonial division. The cause of the pairing is unknown but can be assumed to be due to some sort of mutual attraction between homologous parts. If this force exists, it must be also the same attractive force that brings the homologous chromosomes together later in synapsis with the resulting normal crossing over between the two chromosomes. Therefore, the metaphase plate of the oögonial division, under the influence of the same forces as the later meiotic phase, might be considered a representation in two dimensions of the three-dimensional situation which later is responsible for the characteristic crossover values.

Further evidence for this view can be found in the descriptions of some of the chromosomal aberrations reported in this paper. In these abnormal configurations can be seen arrangements explainable only by the assumption that homologous parts of chromosomes maintain their attractions for each other regardless of changes in inter-chromosomal relationships. There is evidence also, in homologous parts of inverted and corresponding uninverted sections, that the attractive forces oppose each other, since the parts no longer lie in the same order, and destroy any tendency of the two sections to pair normally. The cytological pictures closely parallel the crossover results, further strengthening the view that the oögonial ar-

LEGEND FOR PLATE 1

The oögonial plates were drawn with the aid of camera lucida, using a Bausch and Lomb oil immersion objective, 97× and 1.25 N.A., and Zeiss compound ocular, 30×.

FIGURE 1.—Normal configuration.
FIGURES 2–4.—Salmon.
FIGURE 5.—Dilute-3.
FIGURES 6–9.—Dilute-1.
FIGURES 10–12.—Dilute-2.
FIGURE 13.—Henna with translocation present.
FIGURE 14.—Henna, translocation not present.
FIGURES 15 and 16.—Dilute-5.
FIGURES 17 and 18.—Dilute-4.
FIGURES 19 and 20.—Dilute-6.

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rangement is a real foreshadowing of similar synaptic relationships which result in the crossover values.

Salmon eye color furnishes the clearest evidence for attraction of homologous parts regardless of chromosomal rearrangements. The eye color is associated with a mutual translocation in which, according to the genetic data, one of each pair of the large autosomes contains approximately one-half of the second chromosome and one-half of the third. Crossing over in either of the two large autosomes, when the individual is heterozygous for the mutant condition, is practically normal. According to the primary assumption of attraction of homologous parts, some sort of symmetrical arrangement is to be expected, with one arm of each new chromosome (containing half of the second and half of the third chromosome) tending to pair with the second chromosome, and the other arm tending to pair with the third. Figures 2, 3, and 4 show this arrangement. The mutual pairing of the four large autosomes produces a radial arrangement, seen most strikingly in figure 2. Eleven of the 12 clear plates obtained showed the same arrangement, and incomplete figures indicated a similar configuration. It seems impossible to explain the presence of this characteristic radial arrangement without the assumption that the arms of each composite chromosome are attracted to the homologous arms of the normal second and third chromosomes. That this attraction is strong enough in the synaptic pairing during meiosis to bring about normal crossing over in almost all regions of both chromosomes is shown by the crossover values already discussed.

Cytological findings for Dilute-3 and Dilute-6 best illustrate the effect of inversion on the pairing of homologous parts of chromosomes. In both cases, genetically proved inversions are paralleled by an absence of pairing in corresponding parts of the chromosomal configuration. According to the genetic data for Dilute-3, crossing over occurs normally in the left arm of the second chromosome, and is reduced considerably in the right arm. The assumption is made that an inversion is present in this right arm. In figure 5, a typical configuration for this eye color, two large autosomes are paired normally. The other two are paired only along one arm. The normally paired chromosomes must be the third pair, not concerned with the inversion, and the others, abnormally paired, are the second chromosomes. The inversion in one arm tends to prevent the attraction and therefore pairing of that arm with the homologue in the normal second chromosome.

Dilute-6 genetically has no crossing over along the whole length of the second chromosome; therefore, inversions may have occurred in both

arms. Also translocation of very small fragments from the second to the third and fourth chromosomes occurred. This translocation to the third chromosome, however, does not interfere with crossing over, as shown by the normal frequency. Figures 19 and 20 are representative of the type of plates obtained for Dilute-6. The cytological picture parallels the crossover results. There are two normally paired autosomes, evidently the third pair. The other pair of large autosomes behave as independent bodies. No definite pairing is found to occur along any part of the homologues, just as genetically no crossing over occurs in the second chromosome. It is impossible to determine cytologically that the second has lost any chromatin by translocation to the third and fourth chromosomes. Moreover it is impossible to determine that a third chromosome has received the translocated fragment. The only cytological evidence of translocation is the presence of three fourth chromosomes. Two of them shown in the plates are closely paired and normal in size and position. The other fourth is not distinctly larger but is found to be attracted away from the two that pair together. The presence of the three fourth chromosomes is explainable by non-disjunction of the exceptional chromosome and a normal fourth, followed by the addition of another normal fourth chromosome at fertilization. Cases of this kind have been found by MULLER and PAINTER (1929) and by DOBZHANSKY (1930b). That the genetically found translocations do not appear cytologically is easily understandable if one remembers that in this culture flies appeared not only hyperploid but also hypoploid for the fragments attached to the third and fourth chromosomes. Since very minute fragments are sufficient to prevent hypoploidy, it must be that the translocated pieces here are extremely small, and may easily escape detection due to the compactness of the chromosomes.

With Dilute-1 and Dilute-2 a slightly different situation is encountered. Genetically the condition was explained as a displacement of one arm of the second chromosome to the end of the other arm. In the plates obtained for these eye colors (figures 6–9 for Dilute-1 and 10–12 for Dilute-2), one pair of the large autosomes appears entirely normal, but one member of the other pair has an unquestionably abnormal appearance. The bent portion of this abnormal chromosome is unusually thick and, instead of the normal position, is oriented toward the periphery of the cell. One end of the chromosome is directed toward the center and is pointed instead of knob like. The arm that terminates in the point lies more or less parallel to one arm of the normal homologous chromosome. This is especially true in the configurations for Dilute-2. These consistent differences in appear-

ance and in orientation of the exceptional chromosome agree strikingly with the interpretation from genetic data. Because of its constant orientation toward the center, the pointed end of the abnormal chromosome seems to be the region of spindle-fiber attachment which is included with the right arm in the undisplaced section. Thus the right arm of the chromosome still lies in the same direction as its homologue and their tendency to approach each other especially with Dilute-2 is evidence of the attractive forces exerted between the opposite loci. The left arm seems to be effectively separated from its homologue by the orientation of the right arm and the region of spindle-fiber attachment.

Chromosomal plates for Dilute-4 (figures 17–18) and Dilute-5 (figures 15 and 16) show the occurrence of non-reciprocal translocations involving the second and third chromosomes. Dilute-4 presented particular difficulties because there were very few crossover classes from which to obtain information concerning the nature of the aberration. The translocation involves the right arm of the third chromosome and either arm of the second but it is not known which is the recipient and which the donor chromosome. From six clear plates obtained for Dilute-4, a tentative conclusion can be reached by correlating a few consistent peculiarities with the crossover relationships already discussed. First, the normal arm of the longer chromosome always pairs with its homologue in the normal chromosome, and the left arm of the third chromosome is the only one in which an approximately normal crossover frequency occurs. On this basis it is concluded that the third is the recipient chromosome. In all but one plate, the short donor chromosome lies some distance away from its homologue. Therefore, it is assumed that this is the left arm of the second chromosome in which no crossing over occurred, presumably because of inversion. Consequently it must be the right arm of the second that is attached to the right arm of the third chromosome, reducing crossing over in the latter. The translocated arm, in four of the plates, approaches its homologue in the normal second chromosome. Correspondingly infrequent double crossovers occur in the curved and curved-plexus regions. In the single crossover to the left of curved (a_l d_y b p_r D_l) the curved-plexus-speck region of the normal second chromosome has evidently been exchanged for the part of the translocated piece carrying the Dilute mutation.

Dilute-5 is associated with a translocation of the right arm of the third chromosome to the right arm of the second. In figures 15 and 16 the donor chromosome, the third, can be readily recognized, paired with its homologue in the normal third chromosome. In figure 16, from a large clear cell

in which the chromosomes were not yet fully condensed, the large recipient chromosome pairs abnormally with the normal second chromosome. The end of the longer arm approaches the normal second chromosome, while the central portion of that arm pulls away from the second and approaches one arm of the normal third chromosome. This orientation suggests that the fragment of the third chromosome may be inserted into the right arm of the second chromosome. The tendency is less marked in figure 15 and cannot be seen in some of the other plates. However, the hypothesis furnishes a possible explanation for the total absence of crossing over in the right arm of the second chromosome and the infrequent double crossovers in the right arm of the third. Further genetic and cytological evidence is necessary to prove this theory correct.

DISCUSSION

The eight dominant eye-color mutations discovered among the offspring of radiated Drosophila show several distinct types of association with the accompanying chromosomal aberration. One of the homogeneous eye colors, Henna, proved to be entirely independent of the aberration and seemed to be the result of a point mutation on the third chromosome. It may be either a gene mutation or a very small deficiency (or inactivation of a small amount of chromatin) which produces the dominant phenotypic effect. In either case normal crossing over frequency is possible around the locus of the mutation. The homogeneity of Henna, its definite localization in the chromosome, and its independence of the chromosomal aberration put it in a class with many of the previously known dominant mutations in the second and third chromosomes. So far as is known, this is the first dominant eye-color mutation in Drosophila due to a point mutation that has been reported.

The homogeneous eye color, Salmon, proved to be completely inseparable from the mutual translocation associated with it, and, since normal crossing over occurs in all regions of both composite chromosomes, the point of breakage of one of the chromosomes and the locus of the mutation may be considered identical. This relationship, together with the dominant phenotypic effect with recessive lethal action, is best explained by the hypothesis of gene loss or gene mutation at the point of breakage of the chromosome (MULLER and ALTENBURG 1930). Salmon is similar in its behavior to Punch (MULLER 1930 and OLIVER 1930).

The non-homogeneous dominant eye colors have proved similar to the autosomal eversporting displacements described by MULLER (1930). The same phenomena are associated with all the mutants, dominance with

recessive lethal effect, chromosomal rearrangement (inversion or translocation), and somatic variation. The chromosomal rearrangements made it impossible to find the exact loci of the Dilute mutations but matings with individuals having the Pale-translocation showed that all were located in the plexus-speck region of the second chromosome. Matings of the Dilute-eyed races in all possible combinations have established their allelomorphism at some locus in this region. Plum, Discolored, Tarnished (MULLER 1930) and IcD (OLIVER 1930), also in the right arm of the second chromosome, may prove to be allelomorphic to the Dilute series.

The white locus in the X chromosome that has given rise to the mottled-eye series described by MULLER (1930) is another definitely established locus for the production of non-homogeneous eye color. It has been shown by PATTERSON and PAINTER (1931) that one case is the result of translocation of a small section including the white locus from the X chromosome to one of the fourth chromosomes. The mottled effect of the eye was interpreted as due to the frequent loss of this translocated fragment in embryonic cells. A somewhat similar behavior was noted in Dilute-6 where loss in an early embryonic cell of the small second-chromosome fragment attached to the third chromosome resulted in flies showing the Minute character on only one side of the body. Whether the non-homogeneity of the Dilute eye colors is caused by a similar loss of rearranged chromosome fragments is still undetermined.

Since the oögonial metaphase plates of normal Drosophila females almost always show close pairing of the homologous chromosomes, it has been assumed that the corresponding parts (perhaps the genes) of the homologous chromosomes have some property causing them to exert an attractive force on each other. Cytological examination of the aberrations reported in this paper further strengthens the hypothesis, for pairing of corresponding sections of chromosomes tended to persist in many cases even after one of the sections had been translocated to a non-homologous chromosome. Such behavior can be explained only by assuming attraction of homologous parts of chromosomes regardless of their relative positions in the chromosomal configurations.

The most striking confirmation of the theory of attractive forces comes from the metaphase plates for Salmon eye color where a mutual translocation involving an arm of the second and an arm of the third chromosome resulted in a characteristic radial arrangement of the large autosomes. This arrangement is correlated with normal crossing over in all regions of both chromosomes, a frequency which would be impossible if the trans-

located arms had lost their tendency to pair with their homologues in the normal chromosomes after the rearrangement had occurred.

A distinct correlation also exists between reduction in crossing over due to genetically proved inversions and lack of pairing between inverted and corresponding non-inverted sections of homologous chromosomes. When a section becomes inverted, the genes no longer lie in the same order as the corresponding genes in the normal homologous section. If the attractive forces still exist, as seems certain from the results with Salmon, the resultant effect, due to the conflicting forces between corresponding parts no longer lying opposite each other, would be to nullify the tendency toward pairing of the whole inverted section with its homologue. Dilute-3 and Dilute-6 have this characteristic absence of pairing in inverted sections.

Further correlation between crossing over and chromosomal arrangement is evident in Dilute-1 and Dilute-2 where transfer of one arm of the second chromosome to the end of the other arm has resulted in a chromosome with terminal rather than median spindle-fiber attachment. It is seen that the orientation of the point of spindle-fiber attachment is toward the center in spite of the rearrangement. This determines the abnormal pairing of the homologous chromosomes and consequently the crossover types.

In Dilute-4 and Dilute-5 the exact nature of the translocations is still in doubt but it has been shown that tendencies toward peculiar pairing of the abnormal chromosomes may be helpful in interpreting relationships where the genetic data are insufficient.

The above mentioned correlation between crossing over and the pairing of chromosomes in oögonial stages is understandable when one considers that the attractive forces drawing homologous parts of chromosomes together in oögonial mitotic divisions must be identical with those operating in the later meiotic phases to bring about crossing over between homologous parts of chromosomes. The oögonial configurations can, therefore, be considered fairly clear indications of the type of pairing in the meiotic stages where crossing over actually occurs.

SUMMARY

1. Seven dominant eye colors were discovered among the offspring of males exposed to X-ray irradiation.

2. Of the two homogeneous eye colors, Salmon and Henna, the former proved to be located at the point of breakage of one of the large autosomes

involved in a mutual translocation. The latter is a point mutation in the left arm of the third chromosome.

3. The non-homogeneous Dilute eye colors are all located in the plexus-speck region of the second chromosome, being covered by the translocated piece of the Pale-translocation. They form an allelomorphic series.

All the Dilute eye colors are connected with a chromosomal aberration; Dilute-1, Dilute-2, and Dilute-3 are inseparably associated with inversions in the second chromosome; Dilute-4 and Dilute-5 are connected with non-reciprocal translocations between the second and third; and Dilute-6 has small translocations from the second to the third and fourth chromosomes.

4. Cytological study of chromosome plates of the aberrations shows a definite correlation between crossover classes genetically obtained and the characteristic type of pairing in oögonial cells of the abnormal chromosomes with their homologues. These plates furnish evidence for the existence of attractive forces between homologous parts, exerted not only between the parts of normal chromosomes but also between sections where one of the homologues has been displaced to a non-homologous chromosome.

Due to correlation between crossover classes and pairing or lack of pairing of the abnormal chromosomes, it is concluded that these forces bring about the same type of pairing in the oögonial mitotic phase as they do in the later meiotic phases where crossing over occurs.

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A PARTIALLY FERTILE TRIPLE SPECIES HYBRID IN NICOTIANA

F. A. McCRAY
Harvard University, Forest Hills, Massachusetts

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INTRODUCTION

Crosses between three distinct species in Nicotiana are comparatively rare, only nine having appeared in the literature on this genus. The one here reported upon, (*rustica*×*paniculata*)×*Langsdorffii*, as well as (*rustica*×*Tabacum*)×*paniculata*, and (*rustica*×*paniculata*)×*glutinosa*, was produced in Europe many years ago (EAST 1928) but has not been studied much since. In 1930 KOSTOFF also described such a triple hybrid combination, as well as *Tabacum* var. *sanguinea*×(*Langsdorffii*×*Sanderae*), and listed five others which he had secured, as follows: (*rustica*×*paniculata*)×*Sanderae*, *Tabacum*×(*sylvestris*×*Rusbyi*), *Tabacum*×(*Rusbyi*×*tomentosa*), (*glauca*×*Langsdorffii*)×*Sanderae*, and (*glauca*×*Langsdorffii*)×*alata*. His plants of the (*rustica*×*paniculata*)×*Langsdorffii* combination, however, were sterile and evidently differed fundamentally in chromosome constitution from mine.

It may be noted that in three of the hybrids just listed, two of the *alata-Langsdorffii-Sanderae* group, which cross freely together giving fully fertile hybrids with perfect pairing of chromosomes, are combined with a third species. These three, then, might reasonably be expected to be comparatively easy to secure. In two other cases two of the 12-chromosome *Tabacum*-like species, *tomentosa*, *sylvestris* and *Rusbyi*, are combined with *Tabacum*. In only one other case, (*rustica*×*paniculata*)×*Sanderae*, besides the one here described, do three species having different chromosome numbers enter into the hybrid combination. This combination is very similar to mine, *Sanderae* having the same number (9) of chromosomes as *Langsdorffii*.

MATERIALS AND METHODS

All the plants and seeds used in these investigations were obtained at Bussey Institution, HARVARD UNIVERSITY, where the work was done. Most of the species used had been under observation there for several years and have been described in numerous papers. Authority for all these species is given by EAST (1928). All the plants used were grown in a screened greenhouse, and the usual precautions taken to prevent accidental

crossing. All the pollinations were made by hand except as otherwise noted.

Seeds were germinated in sterilized soil in the seed bench, and the seedlings allowed to grow there until large enough to transplant.

Practically all the material used for cytological studies except root tips was fixed in Allen's modification of Bouin's fluid, B–15, and stained in Haidenhain's haematoxylin. Pollen mother cells were usually examined in Belling's iron aceto-carmine (BELLING 1926) before the buds were fixed in Bouin for the permanent preparations, and in a few instances, which will be mentioned, the observations reported were made from these smears. Some of the root tips were fixed in Flemming's strong solution, and some in Navashin's fixative. A few of these preparations were stained with gentian violet, but usually the haematoxylin was used.

EXPERIMENTS AND RESULTS

In the beginning of the writer's work on this problem he made numerous attempts to combine three species, most of which were fruitless in spite of the fact that in some instances many pollinations were made. The combinations tried, the number of pollinations made, the number of capsules produced, and the viability, if any, in each case are shown in table 1.

In 1928 Doctor D. KOSTOFF gave me two plants of the cross *rustica* var. *humilis*×*paniculata*, presumably the same plants which he had already crossed with *Langsdorffii* to produce his triple hybrids. Upon these two plants I made 12 pollinations with *Langsdorffii* pollen. Five capsules were obtained, containing a small amount of seed. Of 30 seeds planted, 20 germinated. Some of the seedlings were killed by damping off, but 4 (numbers 3, 4, 5 and 6) were raised to maturity. Of a later planting of 10 seeds, only one germinated and this seedling died early.

The four triple hybrid plants, especially 3 and 6 which were more vigorous, were backcrossed to all three parent species, and also selfed. Some capsules were secured from all these combinations. Seeds from these 4 plants backcrossed to *rustica* were planted in October 1930. Of these, 14 germinated and 6 plants were grown, 5 of which were offspring of number 6. These plants were designated 131, 231, 331, 431, and 531. The seeds secured by selfing the triple hybrids failed to germinate when planted at the same time.

The hybrids of *rustica*×*paniculata* have been used in a number of investigations and repeatedly described (EAST 1921, GOODSPEED, CLAUSEN, and CHIPMAN 1926, CHRISTOFF 1928) as have, of course, all the pure species concerned. Much further description seems unnecessary. Briefly, the F_1 is

TABLE 1

Summary of attempts to produce triple species hybrids in Nicotiana.

F_1 HYBRID ♀	♂	NUMBER OF POLLINATIONS	NUMBER OF CAPSULES	VIABILITY OF HYBRIDS
suaveolens× *longiflora*	*plumbaginifolia*	20	..	..
	rustica	6	..	..
	Langsdorffii	136	..	..
	Tabacum var. *macrophylla*	12	..	..
	alata	4	..	..
plumbaginifolia× *Langsdorffii*	*paniculata*	5	..	..
	nudicaulis	8	..	..
suaveolens× *glutinosa*	*Langsdorffii*	111	..	..
	paniculata	39	..	..
	Tabacum	40	..	..
paniculata× *glutinosa*	*Tabacum* var. *macrophylla*	39	..	..
	nudicaulis	14	..	..
	Langsdorffii	147	..	..
	glauca	2	..	..
suaveolens× *plumgaginifolia*	*Langsdorffii*	24	..	..
	Tabacum var. *macrophylla*	2	..	..
paniculata× *Sanderae*	*alata*	15	..	..
	Langsdorffii	29	..	..
	Tabacum macrophylla	2	..	..
	glutinosa	5	..	..
	glauca	7	..	..
nudicaulis× *trigonophylla*	*rustica*	10	..	..
	tomentosa	10	..	..
	Palmeri	12	..	..
rustica× *paniculata*	*tomentosa*	12	..	..
	Palmeri	9	..	..
	acuminata	2	..	..
	trigonophylla	7	..	..
	Rusbyi	6	..	..
	caudigera	6	..	..
	Tabacum angustifolia	7	..	..
	glutinosa	13	1	No germination
	Tabacum macrophylla	23	2	No germination
	caudigera	6	1	No germination
	Tabacum purpurea	9	1	No germination
	glauca	15	12	3 seeds germinated, all died early
	Langsdorffii	12	5	Some matured, partly fertile

intermediate between the parents, perhaps resembling *rustica* somewhat more closely. In figure 1 are shown actual size drawings of typical flowers

for comparison. It will be seen that the flowers of F_1 *rustica*×*paniculata* are intermediate in size and shape between those of the parent species.

The triple hybrid plants were tall, about 36 inches in the greenhouse pots, slender, and branching at the top something like *paniculata*. As already stated plants 3 and 6 were larger and more vigorous than plants

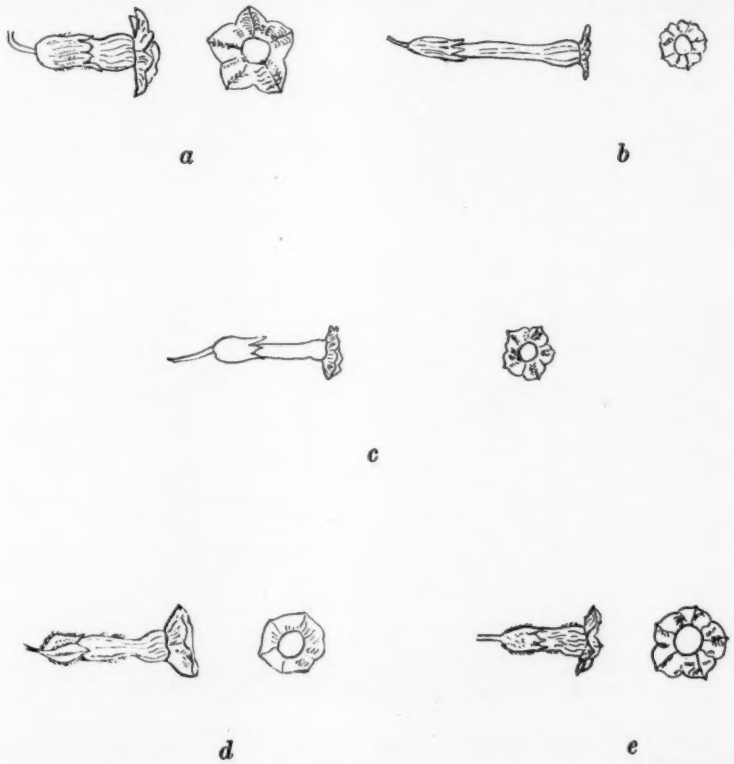

FIGURE 1.—a, flower of *rustica* var. *humilis;* b, flower of *paniculata;* c, flower of *rustica* var. *humilis*×*paniculata;* d, flower of *Langsdorffii;* e, flower of (*rustica*×*paniculata*)×*Langsdorffii.*

4 and 5. The leaves were ovate like *paniculata* in general shape, but acute at the base like *rustica*. They were petiolate.

The flowers were borne in compact panicles with racemose branches, resembling *rustica* somewhat more closely in this respect than did *rustica* ×*paniculata*. The individual flowers, also pictured in figure 1, were shorter than those of the F_1 parent, more like pure *rustica* but more slender.

The absence of any mention of *Langsdorffii* characters will be noted, and it might be thought that the chromosomes of this species failed to enter the combination at all, the "triple" hybrids being produced by the F_1 mother plant parthenogenetically. However, it must be borne in mind that *rustica* and *Langsdorffii* have many characters of leaf, stem, and flower in common, and that the effect of the *Langsdorffii* genes could thus be easily

FIGURE 2.—*rustica*-like derivatives, [(*rustica*×*paniculata*)×*Langsdorffii*]×*rustica*, compared with *rustica*.

masked. More especially is this true since *paniculata* is even more closely related to *rustica* than is *Langsdorffii*, necessitating that any distinctive characters of the latter species might have to overcome the combined effect of inheritance from the other two before they can express themselves in the triple hybrid. Furthermore, the cytological evidence to be presented later will show conclusively that these plants could be neither pure *rustica* nor *rustica*×*paniculata*.

The progeny of plant 6, the result of crossing it with *rustica* pollen, as might be expected, resemble the male parent very closely in all respects, as shown in figure 2. The habit of growth and all detailed characteristics are identical except size. Plants 331 and 431 are considerably smaller and have smaller flowers. But even then there is no more variation than between plants of a pure species when grown under similar artificial (greenhouse) conditions. These *rustica*-like derivatives could not be told from pure *rustica*.

In keeping with this close resemblance to the pure species, these plants exhibit much more fertility than their triple hybrid parent. Plant 131 was pollinated 4 times by each of the three parental species, and its pollen was used reciprocally on each of them 4 times. An equal number of attempts were made to self it. Plants 231, 331, 431 and 531 have been similarly tested, usually 5 pollinations being made in each case, but sometimes a few more. The numbers of capsules harvested are shown in table 2.

TABLE 2

Capsules produced by rustica-like derivatives, ([rustica×paniculata]×Langsdorffii)×rustica.

♀ \ ♂	131	231	331	431	531	SELF	*rustica*	*paniculata*	*Langsdorffii*
131	..	..	..	..	..	3	3	1	1
231	..	..	..	..	..	0	5	4	4
331	..	..	..	..	..	1	3	5	2
431	..	..	..	..	..	4	3	2	3
531	..	..	..	..	..	4	7	5	6
rustica	2	2	3	5	5	..	..	..	..
paniculata	0	0	0	0	0	..	..	..	..
Langsdorffii	0	0	0	0	0	..	..	..	..

In addition, a number of other capsules were produced by natural selfing of 331, 431 and 531.

The number of seeds contained in the capsules included in the table varied considerably. For example, 5 capsules of 331 selfed contained only 4, 5, 5, 5 and 9 seeds. Another group of 5 contained together 72 seeds. In 3 capsules on the same plant pollinated by *paniculata* were found 12, 15 and 71 seeds. Three other capsules pollinated by *rustica* produced 20, 25 and 31 seeds. Likewise several capsules on 531 contained seeds varying in number from 9, in the case of a selfed capsule, to 92, this last one being a capsule of 531×*rustica*.

The viability of these seeds has been tested in three cases. Fifty-one selfed seeds of 331, 80 of 431, and 29 of 531 were planted. Of these 34 or

66.67 percent, 57 or 71.25 percent, and 16 or 55.17 percent, respectively, germinated, and the young seedlings grew normally as long as observed. Naturally it was to be expected that the 5 plants, resembling *rustica* as closely as they did, probably had a nearly complete set of *rustica* chromosomes and would behave in all these crosses very much as pure *rustica* would. That they were not altogether *rustica* in constitution, however, is indicated by the fact that they were somewhat less fertile, producing fewer seeds per capsule, and in some cases, especially in 131 and 431, considerably less than the usual amount of pollen, so that several anthers were necessary to make a good pollination.

Buds and root tips of the 5 plants just discussed have been imbedded for cytological investigation, and may shed some further light on the compatibility of the species involved, or at least on the genetic make-up of the triple hybrid parent.

The cytology of the triple hybrid plants themselves shows pretty clearly, however, how they came into being, and possibly why they were partially fertile while KOSTOFF's were sterile. It should be recalled at this point that, as shown by CHRISTOFF, and by GOODSPEED, CLAUSEN and CHIPMAN, in the F_1 *rustica*×*paniculata* at the metaphase of the reduction division there are usually 12 bivalent chromosomes and 12 univalents, the 12 *paniculata* chromosomes apparently having paired with 12 of the *rustica* chromosomes, leaving the other 12 *rustica* chromosomes as univalents, as is the case in a number of other hybrids in this and other genera. In the anaphase the univalents are distributed to the two poles at random, and appear in the gametes in frequencies from 0 to 12.

If these gametes, then, with 12 to 24 (12+0 to 12) chromosomes should unite with 9 *Langsdorffii* chromosomes, the resulting plants should have 21 to 33 somatic chromosomes. If only 21 are present there should be little or no pairing. CHRISTOFF (1928) states that there is no pairing between *paniculata* and *Langsdorffii* chromosomes in the F_1, and it may be considered doubtful whether the *Langsdorffii* chromosomes would pair with the *rustica* chromosomes, although there seems to be no real evidence on this point. If, however, the larger number (33) of somatic chromosomes (24 *rustica* or *rustica* and *paniculata*+9 *Langsdorffii*) is present there would no doubt be some pairing, and there might be as many as 12 bivalents, reducing the number of chromosomes in I M to 21.

Before describing the actual cytological facts found in these plants let us suppose further that in the F_1 parent the gametic number of chromosomes (12 to 24) should be doubled by failure of a cell wall to form between the granddaughter nuclei. Then when one of these gametes unites with a

Langsdorffii gamete carrying 9 chromosomes the resulting plant should have from 24 to 48+9, or from 33 to 57 somatic chromosomes. In this case most of the chromosomes at I M would doubtless be bivalent, and the total number visible at this phase, assuming complete pairing of all except *Langsdorffii* chromosomes and that they refused to pair at all, would be from 21 to 33 (12 bivalents+9 univalents to 24 bivalents+9 univalents). And since most of the chromosomes are paired there would be nearly as many chromosomes in the II M plates as in the I M plates, especially if the number approaches the maximum, 24 bivalents 9 univalents. Of course there might not be complete pairing of the *rustica* and *paniculata* chromosomes, or a few of the *Langsdorffii* chromosomes might conceivably unite with *rustica*, or with a bivalent, forming a trivalent group. At any rate these theoretical considerations show that the normal expectancy is about 21 to 33 chromosomes in somatic tissues and at I M, and smaller numbers at II M if the two divisions take place in the mother plant as usual; or from 33 to 57 somatic chromosomes with about 21 to 33 appearing at both metaphase stages if, in the megasporogenesis, doubling of the chromosome number has taken place during the second (mitotic) division.

With these possibilities in mind we may examine the available facts in regard to the cytological conditions in the triple hybrid plants. In plant 6, 30 was the most common number of chromosomes observed in the pollen mother cell at both I M and II M. This number was also observed at diakinesis. In different cells counts of from 29 to 33 were obtained at I M, and from 28 to 32 at II M. Two counts of 31 and 30 (?) were also made at I A. The exact number is often difficult to determine because not all the chromosomes lie in the same plane. Several may be a little higher or lower than the equatorial plate. Of the II M plates observed one of the best showed 29 (or possibly 30) chromosomes. Two cells at least showed both II M plates quite plainly. In one the counts were 24 and 24 (or possibly 25); in the other 28 and 28 (or possibly 29). These facts are illustrated in figures 3 and 4, which show I M and II M respectively in plant 6.

This variability in the number of chromosomes is probably due to variability in the amount of pairing, such as has been observed in gametogenesis in a number of F_1 hybrids (compare EAST 1928).

In the anaphase of the reduction division the chromosomes progress to the poles at a rather uneven rate as is typical of hybrids. Figure 5 shows 2 or 3 chromosomes lagging on the spindle at this stage. However, as a rule, all of the chromosomes are included in the nuclei at interkinesis. The same is true of the II A, and the telophase and tetrad stages present quite a normal appearance in most cases, although irregularities were observed

occasionally. Figure 6, for example, shows dyads appearing in the place of tetrads in one of these triple hybrids.

Unfortunately root tip material from this plant was not saved. However it is clear from the amount of pairing shown by the near equality of chro-

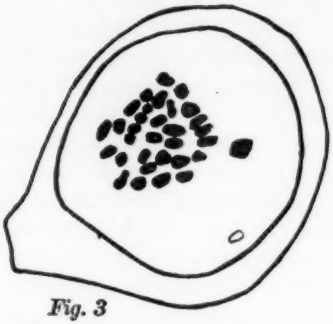

Fig. 3

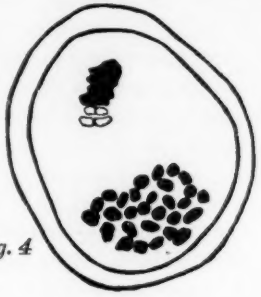

Fig. 4

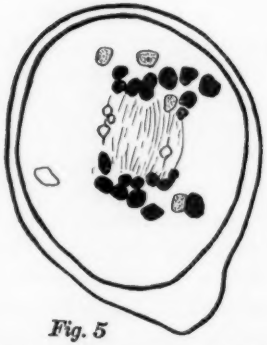

Fig. 5

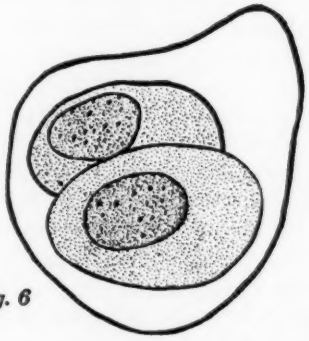

Fig. 6

FIGURES 3–6.—Pollen mother cells of triple species hybrids (*rustica*×*paniculata*)×*Langsdorffii*. FIGURE 3.—I M of plant 6 showing 32 chromosomes, mostly bivalent; one large chromosome, possibly trivalent. FIGURE 4.—II M of plant 6 showing 29 chromosomes in one plate. FIGURE 5.—I A in plant 6. FIGURE 6.—Dyad such as is found occasionally in place of the usual tetrads.

mosome numbers in I M and II M that there must have been over 50 somatic chromosomes.

Plant 3 revealed much the same condition. In both I M and II M the chromosomes line up at the equatorial plate in quite the usual way. Still several chromosomes were often observed above or below. Numerous

plates showing the same range in chromosome numbers as in plant 6 were counted. The early I A was often very irregular (figure 7). Nevertheless in

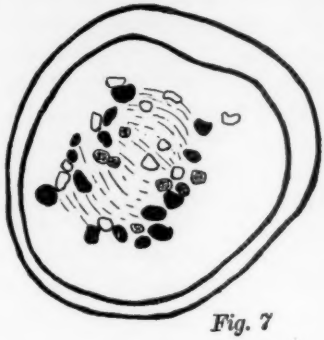

Fig. 7

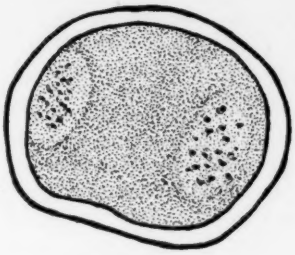

Fig. 8

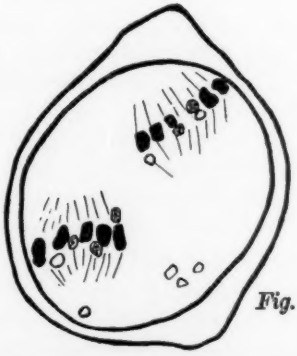

Fig. 9

Fig. 10

FIGURES 7–10.—Chromosome figures of triple species hybrid (*rustica*×*paniculata*)×*Langsdorffii*, plant 3. FIGURE 7.—Occasional irregular anaphase figure. FIGURE 8.—Interkinesis, showing all chromosomes in daughter nuclei; none left in cytoplasm. FIGURE 9.—II A showing both spindles and 4 stray chromosomes, possibly pushed out of place by knife. FIGURE 10.—Root tip cell showing 53 chromosomes.

later stages, as shown in figure 8, nearly if not quite all the chromosomes reach the poles and doubtless enter into the daughter nuclei. An excep-

tional case is shown in figure 9, which represents one pollen mother cell in this plant in which are formed two perfect spindles. Root tip counts also were made for this plant. Figure 10 shows a metaphase plate on which can be seen 53 chromosomes. This being assumed the correct number for this plant where 29 chromosomes appear in I M, they are evidently 24 bivalents+5 univalents. Cells that contain 33 chromosomes are probably of the constitution, 20 bivalents+13 univalents.

DISCUSSION

The chromosome constitution of these triple hybrid plants has already been explained, as a theoretical consideration. All that is necessary, therefore, at this time, is to call attention to the close agreement between the facts as observed and the theoretical possibilities. Plants 3 and 6 at least had over 50 somatic chromosomes, which could be accounted for only by a doubling of the gametic chromosome number in the second division of the megaspore mother cell, and adding to this enlarged number the haploid number of *Langsdorffii* chromosomes. This duplication of many of the chromosomes is just what is necessary to account for the large number of bivalents, which, in turn, is proved by the approximate equality of chromosome numbers in I M and II M. To be sure, this phenomenon could be explained by postulating a double mitotic division of the univalent chromosomes, but there is no evidence to support the idea.

This is the first time, so far as I have found, that doubling during the second division has been reported, although it has often been observed as taking place during the first division.

Of course one can not be sure that all 9 *Langsdorffii* chromosomes went into the make-up of these plants. Some of them may have been eliminated from the fusion nucleus. But from the fact that the maximum number of chromosomes that the F_1 egg cell could have, even after doubling, is only 48, it seems clear that some of the chromosomes in these triple hybrids are indeed *Langsdorffii* chromosomes.

In some of the metaphase figures a few of the chromosomes were larger than the others, and it is possible that these were trivalents. KOSTOFF (1930) concluded that in one of his similar triple hybrids there might be one trivalent and in the other probably four or five. The chromosome numbers he observed in somatic tissues and in pollen mother cells make these suppositions reasonable.

These conclusions regarding gametogenesis of the F_1 *rustica*×*paniculata* agree nicely with data of Doctor W. R. SINGLETON (1932), gathered in his study of the F_2 from selfing the F_1. For example he found one plant

of this second generation having 33 to 36 chromosomes, most often appearing at I M as 19 bivalents and 17 univalents, accounting for 55 somatic chromosomes. Others showed at I M, 18 bivalents and 6 univalents, 14 to 17 bivalents and 14 to 16 univalents, and 35 to 36 bivalents, respectively. In each of these cases, as in mine, it is most likely that one of the gametes, and in the case of the last plant both gametes, must have been diploid. The doubling in these cases however could have taken place during meiosis.

KOSTOFF's triple hybrid plants already mentioned had 24 and 32 somatic chromosomes respectively, and showed 12 to 15 and 14 to 18 chromosomes in the heterotypic metaphase. If, as he supposed, these plants had 1 and 4 or 5 trivalents, then in order to harmonize these observations, there must have been in each case 6 or 7 bivalents, whereas in my plants most of the I M chromosomes were clearly bivalent.

It will also be recalled that KOSTOFF's plants were sterile while mine, at least 3 and 6, were partially fertile. This fertility was probably due to the duplication of chromosomes in the F_1 mother plant which resulted in a preponderance of *rustica* or *rustica* and *paniculata* chromosomes in the triple hybrid plants. That their genetic constitution was of this type is also evidenced by the extremely close resemblance of all the progeny of plant 6, when pollinated by *rustica* pollen, to pure *rustica*, as already noted.

This study affords another instance, of which there are many, of practically pure plants being segregated out of even rather complex crosses, and explains the phenomenon on a cytological basis. It also adds another bit of evidence to that already available on why some plants are so much more fertile than others.

The other triple hybrids which KOSTOFF (1931) has studied cytologically are *Tabacum* × (*Langsdorffii* × *Sanderae*) and *Tabacum* × (*sylvestris* × *Rusbyi*). The former was sterile, but the latter both vigorous and fertile. In this case there was complete pairing of the chromosomes, apparently the 12 from *sylvestris* and the 12 from *Rusbyi* each pairing with 12 of the *Tabacum* chromosomes. This result is not surprising since in both F_1 crosses, *Tabacum* × *sylvestris* and *Tabacum* × *Rusbyi*, the Drosera type of chromosome pairing is observed, there being in each case 12 bivalents and 12 univalents at I M. It is perhaps doubtful however, as Doctor E. M. EAST points out, whether these facts should be taken to mean that half of the *Tabacum* chromosomes are homologous to *sylvestris* and the other half to *Rusbyi* chromosomes. GOODSPEED and CLAUSEN (1928) conclude that the *Tabacum* chromosomes are half *sylvestris* and half *tomentosa* from similar reasoning in regard to their hybrids, *sylvestris* × *Tabacum*, *tomentosa* × *Tabacum*,

and *sylvestris*×*tomentosa*. Obviously both these conclusions can not be sound unless, indeed, the *Rusbyi* and *tomentosa* chromosomes are practically identical. This is doubtful even though the species are quite similar. In my tests *Rusbyi* failed to produce any hybrids with *tomentosa* pollen after 5 trials. This is admittedly not positive evidence. But it must also be borne in mind that *Tabacum* also shows a similar type of chromosome behavior with *glutinosa*, as well as with *sylvestris*, *Rusbyi* and *tomentosa* and probably with *glauca* and *Sanderae* (EAST 1928). At least if both these conclusions as to the homology of chromosomes in the different species are correct, the identity of several chromosomes in all these 12 chromosome species should be established. Evidently pairing does not necessarily mean homology of chromosomes. In fact YARNELL (1931) was able to demonstrate pairing of non-homologous chromosomes in Fragaria.

SUMMARY

1. A triple species hybrid was produced by using *Langsdorffii* pollen on F_1 *rustica*×*paniculata*. Four plants, numbered 3, 4, 5 and 6, were grown, which resembled the F_1 parent in being intermediate between *rustica* and *paniculata*, but which, in certain respects, were more like *rustica*. No distinctive *Langsdorffii* characters were found, but it is pointed out that *Langsdorffii* and *rustica* have many resemblances, as do also *rustica* and *paniculata*, so the absence of definite *Langsdorffii* characters does not mean that the chromosomes of this species were left out, fertilization being replaced by parthenogenesis.

2. A cytological study of these triple hybrid plants, especially of one of them, bears out this conclusion, and affords an additional explanation of the lack of *Langsdorffii* characters. The somatic chromosome number is so large, over 50, it can be accounted for only by assuming doubling of the chromosome number in the second division of megasporogenesis in the F_1 female parent. This doubled number, 24 to 48, plus 9, the haploid number in *Langsdorffii*, gives 33 to 57 as the expected number of chromosomes in the triple hybrid. If the actual chromosome number is near the upper limit of this range, the few *Langsdorffii* chromosomes present would have many *rustica* and *paniculata* factors to overcome before the characters of this species could be expressed.

3. These chromosome numbers were found in plants 3 and 6. The best root tip plate in plant 3 showed 53 chromosomes. A variable amount of pairing in pollen mother cells caused these chromosomes to appear at I M as 27 to 39, or more often 29 to 33. Since nearly all of these chromosomes were bivalent, II M plates also showed 28 to 32 chromosomes.

4. These two plants, 3 and 6, were more vigorous and fertile than the others, which were not studied cytologically. Possibly plants 4 and 5, like KOSTOFF's similar sterile plants, were less successful because of having resulted from the union of haploid gametes so there was a less complete set of *rustica* chromosomes.

5. Capsules were produced when these triple species hybrid plants were pollinated by each of the three pure species, and also when selfed. Seeds of number 6×*rustica* germinated well and vigorous plants closely resembling *rustica*, and at least partially fertile, were grown. These produced numerous capsules when pollinated by all the parent species and when selfed. Selfed seed of three of them germinated, and the seedlings grew normally as long as observed.

ACKNOWLEDGMENT

The writer wishes to express his indebtedness to Doctor E. M. EAST for plants and seeds which he kindly furnished in his laboratory, and especially for his helpful criticisms and suggestions given in connection with the experiments described.

He is also indebted to Doctor D. KOSTOFF for the F_1 plants which served as the immediate parents of the triple hybrid.

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FURTHER STUDIES ON THE GENETICS OF ABNORMALITIES APPEARING IN THE DESCENDANTS OF X-RAYED MICE

C. C. LITTLE AND B. W. McPHETERS
Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine

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In 1923 the senior writer and BAGG described the occurrence of abnormalities of the eyes and limbs of mice descended from animals which had been treated with X-rays. It was shown that these abnormalities were inherited. The object of the present communication is to present data on the type of inheritance involved and to describe certain of the results of selection upon the development of the character.

NATURE OF THE ABNORMALITY

BAGG and the senior writer (1924) gave a preliminary description of the eye abnormality. It was found that one or both eyes might be affected. In 227 defective eyes the following grades of abnormality were listed:

Slight atrophy of eyelids	12
Marked but not complete atrophy of eyelids	114
Eyelids completely missing	101
Eyes slightly atrophic, no corneal opacity	45
Eyes slightly atrophic, marked corneal opacity	36
Eyes markedly atrophic, no corneal opacity	146

The anatomical changes associated with the eye abnormalities include various degrees of atrophy of the optic tract culminating in its complete disappearance. The skull may be asymmetrical, being twisted toward the side of the head containing the abnormal eye. The diameter of the orbit is sometimes reduced.

The limbs show many different types of abnormality. Of these the commonest is a club-foot condition. The digits are often flexed and fused. The bones of the metatarsus and phalanges may be appreciably shortened. The digital muscles may also be much atrophied.

As the number of animals recorded increased, varying degrees of polydactyly were also encountered and described. BEAN (1929) listed certain of these types and pointed out that a single foot could show multiple abnormalities. She cited one example in which the basic characteristics of polydactyly, brachydactyly, and syndactyly were all present. The most

consistent defect found by her was the reduction, by fusion, of the number of carpals or tarsals. BAGG (1929) in examining a large number of abnormal limbs lists the following numbers of various manifestations of the character.

1.	Club feet with dorsal flexion and syndactylism	291
2.	Club feet with palmar flexion and syndactylism	9
3.	Club feet with marked distortion of entire foot	6
4.	Syndactylism without abnormal flexion	9
5.	Hypodactylism	27
6.	Congenital amputation	16
7.	Polydactylism	93

The next step in investigating the true nature of the character was to trace its appearance in embryonic development. This was begun by BAGG who published in 1924 figures showing that there are present, during the latter part of pregnancy, in embryos destined to become abnormal, extensive hemorrhagic lesions. These lesions have an etiological relationship to the structural abnormality of the eye. The lesions are late in pregnancy full of extravasated blood. BAGG concludes that there is apparently "a relation between the presence of a defective blood vascular system in the embryos and the later arrested development of the abnormal organs." He indicates that the presence of hemorrhagic lesions on the feet of certain embryos may mean that abnormalities of the limbs also have a similar origin. In 1929 the same investigator described the origin of the foot abnormality as follows:

"Between the twelfth and thirteenth days of prenatal life there occurs a localized arrest in development of a part of the foetal foot which is associated apparently with a perivascular lymph stasis almost always on the dorsum of the foot. This condition results in the formation of a well-defined bleb, or blister-like area, in the subcutaneous tissue of the foot which is filled with a clear amber-colored fluid. The next step . . . is the escape of blood into the bleb and, in consequence, the formation of a well-defined hemorrhagic lesion."

Our knowledge of the origin of the abnormality has been greatly increased by the recent work of BONNEVIE (1931). She confirmed the results of BAGG with older embryos (15–25 mm) but finds that the conditions described by him are a secondary stage in the development of the anomalies. She states: "In the younger embryos (9–11 mm) clear blebs are found also on the median dorsal part of the embryo, especially across the shoulder

region as well as on the hind part of the body. At the head clear blebs are at this stage often found resting on the upper jaw."

"Still earlier embryos (7–9 mm) have no blebs at all on the distal part of their feet while on the back of their body the blebs may be very large. Two embryos were found with blebs covering their whole back and others in which the blebs of the shoulder region were prolonged in the direction of one of the fore feet. The blebs of the hind part of the back are often seen to be continued on the broad root of the embryonic tail, and in somewhat older embryos (9–11 mm of length), isolated blebs are very often found along the dorsal side of the tail."

She continues by pointing out that the gradual change in the localization of the blebs seems to indicate a mechanical displacement of fluid, first appearing at some place in the median dorsal line of young embryos. The amniotic membrane may help by pressure in this process of displacement. Blood lesions never arise at points where the blebs are passing by but only where they are arrested. Bleeding probably occurs from the underlying capillaries. The shoulder blebs move down into the limbs causing lesions there. The discrepancy between lesions of the right and left front feet noted by BAGG (1929) and MURRAY (1929) is probably accounted for by a mechanical factor—the curling up of the embryo in a spiral. The direction of the spiral is in the great majority of cases right sided. This would give a greater opportunity for left front foot abnormalities.

In the unselected material tabulated by BAGG and by MURRAY the total incidence of abnormalities of the left front foot was 772 and of the right front foot 464. BONNEVIE believes that the existence of more frequent abnormalities in the front limbs as compared with the hind limbs is due to the escape and disappearance during ontogeny of a number of posterior blebs via the tail.

The origin of the clear fluid which fills the blebs is of great interest. As far as BONNEVIE'S work extends the origin of the fluid seems to be cerebrospinal and not lymphatic as suggested by BAGG. BONNEVIE adopts as a working hypothesis the conclusion that the fluid accumulates inside the medullar tube causing swelling of the myencephalon region. From this center the blebs are distributed, some being resorbed while others remain to cause anomalies. The investigation is being continued.

In view of the nature of the abnormality as shown by these morphological studies the earlier genetic symbol *h* (hemorrhagic lesion) used by the writer (1924) to describe it had probably better be replaced by M^{BL} for normal and m^{bl} (myencephalic blebs) for the abnormal types.

THE GENETICS OF THE ABNORMALITY

In 1923 soon after the appearance of the abnormality the writer and BAGG reported that it followed the general genetic behavior of a Mendelian recessive. There were, however, produced from matings of abnormal×abnormal 374 abnormals and 73 normals. This means that 16.3 percent of these mice, supposedly genetic abnormals $m^{bl}m^{bl}$, were normal in appearance. In 1924 the numbers had been increased to 594 abnormals and 132 normals, a percentage of 18.1 normal overlaps. A number of these were bred together and gave a total of 106 abnormal, 42 normal young. In this case the percentage of "normal overlaps" had been raised to 28.3.

During the past eight years selection of various sub-strains of the abnormality have been carried on by the writer.

Two main sub-strains, one in the direction of increased proportion of eye abnormalities, the other in the direction of increased proportion of normal overlaps, have been developed. The former of these is designated as Line "700," the latter as Line "9000A." To the results recorded by the writer (1931) additions have been made which now may be tabulated as follows:

TABLE 1

LINE 9000A				LINE 700					
GENERATION OF SELECTION	NORMAL	ABNORMAL	PERCENT ABNORMAL	GENERATION OF SELECTION	NORMAL	ABNORMAL EYE	PERCENT ABNORMAL EYE	ABNORMAL FEET	PERCENT ABNORMAL FEET
1	44	0	0.0	1	10	74	88.0	1	1.2
2	40	3	7.0	2	8	97	92.3	0	0.0
3	62	1	1.6	3	6	104	94.5	0	0.0
4	160	2	1.3	4	8	86	91.2	0	0.0
5	184	0	0.0	5	7	44	86.2	0	0.0
6	112	0	0.0	6	3	23	88.4	0	0.0
7	131	0	0.0	7	3	49	94.2	0	0.0
8	71	0	0.0	8	7	48	87.2	1	1.9
9	80	0	0.0						
Total	884	6	0.7	Total	52	525	90.9	2	0.4

From table 1 it is easily seen that the two strains have been separated by selection so that for the last five generations in Line 9000A there have been no abnormals while in Line 700 the percentage of abnormals over eight generations is 90.19. At the same time Line 700 has practically been freed from the foot abnormality (see table 1).

TABLE 2

LINE 9000B				LINE 9000C			
GENERATION OF SELECTION	NORMAL	ABNORMAL LIMBS	PERCENT ABNORMAL LIMBS	GENERATION OF SELECTION	NORMAL	ABNORMAL LIMBS	PERCENT ABNORMAL LIMBS
1	8	29	78.3	1	6	27	81.8
2	3	43	93.4	2	5	39	88.6
3	21	108	83.7	3	6	62	91.1
4	7	76	91.5	4	9	84	90.3
5	0	55	100.0	5	1	48	97.9
6	2	81	97.5	6	2	41	95.3
7	0	48	100.0				
Total	41	440	91.4	Total	29	301	91.2

TABLE 3

LINE 9000B

GENERATION OF SELECTION	ABNORMAL FRONT ONLY		ABNORMAL FRONT AND HIND		ABNORMAL HIND ONLY	
	NUMBER	PERCENT	NUMBER	PERCENT	NUMBER	PERCENT
1	15	57.6	9	34.6	2	7.6
2	23	53.4	17	39.5	3	6.9
3	43	39.8	55	50.9	10	9.2
4	34	44.7	36	47.3	6	7.8
5	28	50.9	25	45.4	2	3.6
6	44	54.3	36	44.4	1	1.8
7	25	52.0	22	45.8	1	2.0
Total	212	48.5	200	45.7	25	5.7

LINE 9000C

GENERATION OF SELECTION	ABNORMAL FRONT ONLY		ABNORMAL FRONT AND HIND		ABNORMAL HIND ONLY	
	NUMBER	PERCENT	NUMBER	PERCENT	NUMBER	PERCENT
1	5	17.2	15	51.7	9	31.0
2	5	12.8	20	51.2	14	48.2
3	12	19.3	32	51.6	18	29.0
4	25	29.7	38	45.2	21	25.0
5	15	30.0	21	42.0	14	28.0
6	13	31.7	20	48.7	8	19.5
Total	75	24.5	146	47.8	84	27.5

If Line 9000A is analyzed as to the nature of the abnormality it is found that of the 6 abnormals, 4 had abnormal feet and 5 had abnormal eyes. In other words, 99.4 percent had normal eyes and 99.5 percent normal feet.

Lines 9000B and 9000C are additional sub-strains in which selection has been carried on for increase in incidence of foot abnormalities. They are closely related in origin to Line 9000A.

The incidence of limb abnormalities in these lines in succeeding generations of selection is given in table 2.

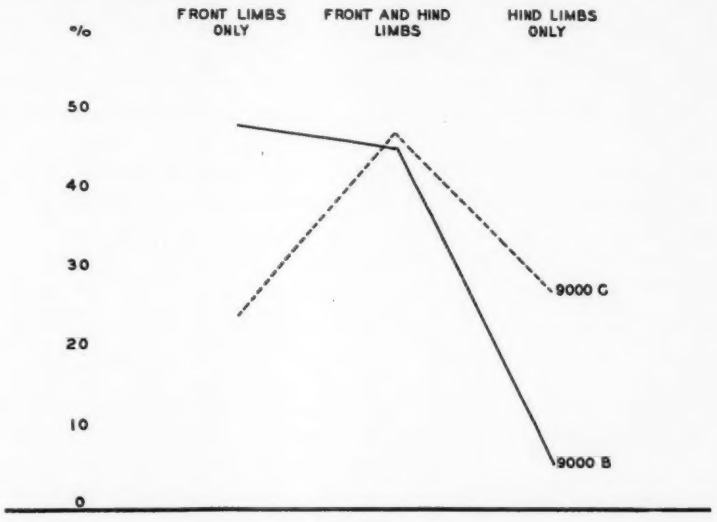

FIGURE 1.

The incidence of the "abnormal limb" character may therefore be greatly increased by selective breeding. In Line 9000B selection has been toward abnormalities of the front feet; in Line 9000C it has been in the direction of abnormality of the hind feet. Table 2 shows that while progress in separating the two locations of foot abnormalities has been slow there has been a distinct increase in the percentage of animals with abnormalities in the front or hind feet or in both. Localization is therefore difficult but increase in the percentage of total foot abnormalities has been successful. BAGG in 1929 reports the incidence of foot abnormalities in his stock in 432 animals out of 5280. He says that the incidence of foot abnormalities can be "greatly increased" by selection. MURRAY (1929), using the basic stock from which the writer took his material for Selection Lines 9000B and

9000C, reports that out of 1922 animals 356 or 18.5 percent had abnormal feet and 1212 or 63 percent abnormal eyes.

That there has been established some sort of difference between Line 9000B selected for front limb abnormalities and Line 9000C selected for hind limb abnormalities is shown by table 3.

In Line 9000B the results of seven selection generations give 48.5 percent of the foot abnormalities in the front limbs only. In Line 9000C the percentage for six selection generations is 24.5. On the other hand Line 9000C gives 27.5 percent with abnormalities in the hind feet only while Line 9000B has only 5.7 percent. There is then evidence (graphically shown in figure 1) of some progress in the direction of selection. The fact that the sixth selection generation of Line 9000C makes the poorest showing is not encouraging but may simply mean a chance deviation due to small numbers.

The occurrence of eye abnormalities in Lines 9000B and 9000C is also a matter of interest. Table 4 gives the results for the two groups.

TABLE 4

Line 9000B

GENERATION OF SELECTION	RIGHT EYE ABNORMAL	LEFT EYE ABNORMAL	BOTH EYES ABNORMAL	TOTAL ABNORMAL	NORMAL	PERCENT ABNORMAL
1	6	10	10	31*	6	83.7
2	17	20	5	42	4	91.3
3	51	49	17	117	10	92.1
4	42	27	6	75	8	90.3
5	22	24	3	49	5	90.7
6	22	38	14	74	9	89.1
7	22	20	2	44	4	91.6
Total	182	188	57	432	46	90.3

* There were five abnormal-eyed individuals of this generation in which the location of the eye abnormality was not recorded.

Line 9000C

GENERATION OF SELECTION	RIGHT EYE ABNORMAL	LEFT EYE ABNORMAL	BOTH EYES ABNORMAL	TOTAL ABNORMAL	NORMAL	PERCENT ABNORMAL
1	6	9	10	25	8	75.7
2	16	15	11	42	2	95.4
3	23	25	10	58	10	85.2
4	34	39	7	80	13	86.0
5	23	14	2	39	10	79.5
6	9	13	7	29	14	67.4
Total	111	115	47	273	57	82.7

The high degree to which the incidence and type of eye abnormality in strains 9000B and 9000C have paralleled those in Line 700 is further shown by the distribution of the abnormality. This is as follows (table 5).

TABLE 5

	RIGHT EYE ABNORMAL	PERCENT	LEFT EYE ABNORMAL	PERCENT	BOTH EYES ABNORMAL	PERCENT
Line 700	250	44.8	241	43.2	66	12.0
Line 9000B	182	42.6	188	44.0	57	13.4
Line 9000C	111	40.6	115	42.1	47	17.3

From the close correspondence of the figures in the three strains it is evident that the production and distribution of eye abnormalities is proceeding along the same general line in each case and is the result of the same morphogenetic process.

The distinctly lower percentage of abnormal eyes in Line 9000C, especially in the sixth generation, suggests evidence in support of the idea that gradually we may be getting rid of the abnormality at the anterior end of the body in that line. Further selection will, however, have to be carried on before this fact can be established.

The facts clearly evident are:

1. It is possible to obtain a line (700) high in eye abnormalities, 90.9 percent, and practically free from visible foot abnormalities, 0.4 percent.
2. A line (9000B) high in anterior limb abnormalities, 91.4 percent, is also high in eye abnormalities, 90.3 percent.
3. A line (9000C) relatively higher in posterior limb abnormalities is lower in eye abnormalities (82.7 percent total; 67.4 percent for the sixth selection generation).
4. A line (9000A) can be selected which is low in both eye (0.56 percent) and limb (0.45 percent) abnormalities.

These results show that progress has been made in isolating different degrees of the abnormality in different genetic sub-strains. The greatest degree of abnormality is found in Lines 9000B and 9000C. As the degree of abnormality is lessened the eyes seem to be the last portion of the body from which it disappears.

There is an interesting analogy with piebald spotting in this respect. In mice one of the best examples of persistent localized spotting is found in the white-faced race described by DUNN (1925). Definite persistence of a white forehead characterizes this strain. In out-crosses there is expressed a strong genetic tendency for the spotting to reappear on the forehead.

Localization therefore seems to be strongly established as is that of the eye abnormality above considered.

OUT-CROSS EXPERIMENT

After selection had clearly established in Line 700 a strain high in eye abnormalities it was thought that an out-cross to determine the nature of the inheritance of the abnormality would be desirable.

As a normal parent MURRAY'S strain of LITTLE dilute browns was chosen. Reciprocal crosses were made. A total of 143 F_1 animals, all normal, was obtained.

The two F_2 generations gave a total of 1206 young shown in table 6.

TABLE 6

CLASS OF PROGENY	F_2 dB_T ♀ × ABNORMAL ALBINO ♂	F_2 ABNORMAL ALBINO ♀ × dB_T ♂	TOTAL	EXPECTED 9: 3: 3: 1 UNCORRECTED
Colored normal	382	398	780	678.3
Colored abnormal	79	70	149	226.1
Albino normal	110	113	223	226.1
Albino abnormal	21	33	54	75.4
Total	592	614	1206	

Since inbred abnormals of Line 700 gave 9.1 percent normal overlaps (see table 1) it seemed entirely proper to correct for that figure and to consider that the actual number of abnormals obtained represented 90.9 percent of those which were actually genetically abnormal. Table 7 shows the data after this correction has been made.

TABLE 7

CLASS OF PROGENY	F_2 dB_T ♀ × ABNORMAL ALBINO ♂	F_2 ABNORMAL ALBINO ♀ × dB_T ♂	TOTAL CORRECTED	EXPECTED 9: 3: 3: 1 UNCORRECTED
Colored normal	377	392	769	678.3
Colored abnormal	86	76	162	226.1
Albino normal	108	110	218	226.1
Albino abnormal	23	36	59	75.4

It is clear that there is still a marked deficiency in the number of abnormals observed when compared with expectation. The simplest way to explain this is by hypothesizing differential mortality during embryonic life. The ratios given in tables 6 and 7 were based on counts made at birth.

In order to study the ratio *in utero* 33 pregnant F_1 females were killed. An examination of the embryos showed the following classes: colored normal, 186; colored abnormal, 34; albino normal, 48; albino abnormal, 16; *dead and disintegrating*, 25.

The presence of the twenty-five disintegrating embryos gives the probable clue as to what has happened to a considerable number of abnormal embryos. In most of the disintegrating embryos the process had proceeded so far that classification according to abnormal or normal was impossible. All those that could be identified however were abnormal. It is therefore reasonable to suppose that the group of degenerating embryos is in reality an abnormal class which should be added to the other recorded abnormal groups. In the data derived from litters examined *in utero* there were observed 234 normal and 50 abnormal young. The expected Mendelian proportions are 223 normal and 71 abnormal. If the twenty-five degenerating embryos are added to the abnormal group the numbers become 234 normal and 75 abnormal. A further correction of 9.1 percent of the non-degenerated abnormals recorded is also to be made. This would amount to approximately 4 animals. This would produce a final corrected result of 230 normal 79 abnormal. The expectation is 231 normal and 77 abnormal. The degree of resemblance between corrected observation and the Mendelian expectation is strikingly close.

If we next consider again the F_2 data to which reference has already been made, we shall have to apply to the original data the same two corrections as have already been utilized for the litters recorded *in utero*. The results of doing this are as follows (table 8):

TABLE 8

	NORMAL	ABNORMAL
Observed data uncorrected	1003	203
Expected on 3:1 ratio	904.5	301.5
After correction for "normal overlaps"	984.5	221.5
After correction for embryonic mortality	984	323
Expected on basis of correction	980	327

In applying the correction for embryonic mortality the *in utero* litters have been used as a standard. These showed clearly that for every two abnormal embryos which gave promise of reaching birth in an identifiable condition, there was one that degenerated. The birth ratio of abnormals may then be taken as representing approximately two-thirds of the number

actually formed. The difference may well be accounted for by differential mortality.

The question naturally arises as to whether the high embryonic mortality found in descendants of the Line 700 out-cross also exists in the Lines 9000A and 9000B which are related to Line 700. The opportunity has not yet presented itself to study large numbers of pregnant females. Those studied, however, show no embryonic mortality in Line 9000A and a considerable degree of mortality in *utero* in Line 9000B. Since the latter line is genetically homozygous for the abnormality it follows that certain abnormal individuals die before birth even when no competition with normal embryos is involved. Variation within the genetically abnormal embryos may be considered as constitutional in nature. Competition between normal and abnormal embryos *in utero* is environmental. The two types of factors are operative in producing the high embryonic mortality recorded in the F_2 generation of the out-cross.

LINKAGE TESTS

It is also interesting to determine whether or not any evidence exists for linkage of the abnormality with the genes for albinism, *c*, agouti, *A*, black, *B*, and intensity, *D*, with which it was introduced into the cross.

In order to determine this point the data for the inheritance of each of these pairs of allelomorphs must be tabulated separately.

The situation as regards dilution is as follows. The abnormal individuals are $DDm^{bl}m^{bl}$ in constitution; the dilute brown normals are $ddM^{BL}M^{BL}$. The F_1 generation is therefore $Dm^{bl}dM^{BL}$. In F_2 the intense normal DM^{BL} and dilute abnormal dm^{bl} types are crossover classes, while the intense abnormal Dm^{bl} and dilute normal dM^{BL} are linkage classes. The actual numbers obtained after correction for "normal overlaps" and embryonic mortality are as follows.

	Crossover Normal intense	*Linkage Normal dilute*	*Linkage Abnormal intense*	*Crossover Abnormal dilute*
Observed	516	162	124	67
Expected	486	162	162	54

Of the two linkage groups one is slightly lower than expected; the other is equal to expectation. Both crossover groups are higher. There is certainly no evidence of linkage.

The black gene is introduced along with the abnormality, the brown with its normal allelomorph. The cross is therefore $BBm^{bl}m^{bl} \times bbM^{BL}M^{BL}$. The F_1 generation is $Bm^{bl}bM^{BL}$ in formula. The F_2 corrected figures and expectation follow.

	Observed	*Expected*	
Black normal (crossover)	525	486	Higher
Brown normal (linkage)	161	162	Equal
Black abnormal (linkage)	128	162	Lower
Brown abnormal (crossover)	61	54	Higher

Again the crossover classes are higher than those showing linkage.

Agouti is absent from certain of the F_1 animals so the total numbers will be smaller than in the preceding crosses.

	Observed	*Expected*	
Agouti normal (crossover)	302	297	Higher
Non-agouti normal (linkage)	111	99	Higher
Agouti abnormal (linkage)	84	99	Lower
Non-agouti abnormal (crossover)	25	33	Lower

One linkage class is higher than expectation, one lower. One crossover class is also higher and one lower than their expected quota.

Color and albinism are easily recorded at birth so that the numbers will be higher than in any of the preceding crosses. The cross was made as follows: Colored normal $CCM^{BL}M^{BL}$ × albino abnormal $ccm^{bl}m^{bl}$. F_1 is therefore $CM^{BL}cm^{bl}$.

The F_2 corrected results and expectation follow.

	Observed	*Expected*	
Colored normal (linkage)	767	720	Higher
Colored abnormal (crossover)	212	240	Lower
Albino normal (crossover)	218	240	Lower
Albino abnormal (linkage)	86	80	Higher

Both linkage classes are higher than expectation and both crossover classes are lower.

When a χ^2 test is applied to these figures the probabilities are a little more than 3 chances out of 100 that random sampling will explain the results. The deviation of the four classes however shows that the ultimate recessive, or $ccm^{bl}m^{bl}$ group, departs very slightly from expectation. If a clear-cut case of linkage was involved this class should have been as much in excess as is the $CCM^{BL}M^{BL}$ group. Such is not the case. The final test of linkage must therefore await further experimentation.

OCCURRENCE OF FOOT ABNORMALITIES IN F_2 MICE

Among the 203 F_2 abnormals recorded at birth there were seven with abnormal feet. This is a percentage of 97.0 normals and 3.0 abnormals. It is doubtful whether this is significantly different from the record of the pure "700" stock. In this case there were 99.6 percent normals and 0.4 percent

abnormals. Whether there is a minor difference of some real significance between them cannot be determined from the numbers obtained. It is however certain that the increase in foot abnormalities is in no way comparable to the results which would have been obtained did the incidence of foot abnormalities depend upon a large number of modifying genes present in normal stocks but eliminated by selection from Line 700.

It will be remembered that CASTLE obtained a release from the result of selection of modifiers when he crossed his selected hooded rats with wild stock. No such result is here obtained in the out-cross with normal. This suggests that the reduction in foot abnormalities seen in Line 700 has been accomplished by some sort of change in the abnormal gene m^{bl} or by perhaps a single modifier which both Line 700 and, by chance, the dilute brown normal strain used possess.

The relation of the eye abnormality to that of the limbs will require further study. It is clearly a complex matter involving not only genetic but morphogenetic analysis. The isolation of a line ("700") in which the incidence of limb abnormalities is reduced to a minimum (0.4 percent) is important. The fact that up to now an increase in limb abnormalities by selection has been accompanied by an increase in eye abnormalities suggests that limb abnormalities are a secondary step in the process of bleb formation. As far as the data presented here are concerned limb abnormalities seem to be the result of an excess or overflow of bleb-forming activity which extends beyond the degree of that process necessary to form abnormal eyes. Further selection on the hind limb-abnormal Line 9000C may show that bleb formation influencing the posterior limbs but not the anterior can be separated off as a distinct morphogenetic and genetic process. At present however the results of selection have not reached that point.

CONCLUSIONS

1. The abnormality under consideration in its earliest recognized form consists of a swelling of the myencephalon in embryos 7–9 mm in length. This swelling gives rise to a number of blebs full of colorless fluid (BONNEVIE 1931). It is given the symbol m^{bl} (myencephalic blebs).

2. In its later stages the abnormality consists in deformities of eyes and limbs which follow arrests in development caused by local blood-filled blebs which distort and disturb normal symmetrical development by pressure (BAGG 1929).

3. The abnormality is inherited as a Mendelian recessive. In a line ("700") selected for high incidence of abnormal eyes there is 9.1 percent

overlap with normal. Limb abnormalities in this line occur in 0.4 percent.

4. By selective breeding of the descendants of normal overlaps, a line (9000A) has been established in which the incidence of abnormals has been reduced to 0.7 percent.

5. By selective breeding the incidence of limb abnormalities has been increased in two lines, 9000B (91.42 percent) and 9000C (91.2 percent).

6. Simultaneously these two lines have shown a distinct increase in the incidence of eye abnormalities until they have reached a point which compares favorably with line 700 (90.9 percent) selected for that purpose, Line 9000B (90.3 percent), and Line 9000C (82.7 percent). The distribution of eye abnormalities in these lines is practically identical with that seen in Line 700, the high eye-selection line.

7. When abnormal albino animals from Line 700 are crossed with normal colored mice from the MURRAY derivative of the LITTLE dilute brown (db_r) stock, the F_1 is all normal. The F_2 shows a 9:3:3:1 ratio with a significant deficiency of abnormal mice.

8. Besides the correction for normal overlap, 9.1 percent, studies of embryonic ratios *in utero* show that approximately 8 percent of the embryos degenerate *in utero*. Whenever identification of these has been possible, they have proved to be abnormals. The numbers obtained make a correction appear necessary. The incidence of degenerating embryos is sufficiently high to amount to one-half of the living abnormal embryos.

9. When corrections of the numbers for these two modifying agents are made the ratios obtained fit the Mendelian expectation closely.

10. When the separate factors are studied to determine possible linkage relations with the abnormal gene m^{bl} they all show clearly random segregation with the exception of the *Cc* pair of allelomorphs. In this case there is evidence of linkage which however must be tested by a backcross generation before being considered conclusive.

11. The low incidence of foot abnormalities in F_2 mice indicates that the abnormal-eyed parent line ("700") has not been developed by the gradual selection of many modifiers but by some other genetic process.

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INHERITANCE OF MONOSOMICS IN *NICOTIANA RUSTICA*

W. E. LAMMERTS[1]

California Institute of Technology, Pasadena, California

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Comparatively few investigations have been concerned with a study of monosomics ($2n-1$ types) and their mode of inheritance. The only extensive work is that of KIHARA (1924) and NISHIYAMA (1928) in Triticum and the analysis of the monosomics fluted and corrugated in *Nicotiana Tabacum* by CLAUSEN and GOODSPEED (1926). In these cases $n-1$ pollen grains rarely functioned and selfing gave substantially the same results as backcrossing. Accordingly WATKINS (1925) and CLAUSEN (1926) both argued that the rapid return to parental chromosome number of the derivatives obtained by selfing hybrids showing the Drosera type of reduction division was largely due to this phenomenon. Gametic elimination, selective functioning of ovule classes and zygotic elimination were not necessarily involved or at least played a minor role. Similarly selfing of plants obtained by backcrossing the F_1 *rustica-paniculata* hybrid to *N. rustica* (24_{II}) resulted in a return to the chromosome number of that species (unpublished data). A study of as large a series of monosomics as possible was undertaken with the idea of determining whether the results of the above investigators in other genera and species were applicable here. An unexpected amount of variation in the behavior of individual monosomics was disclosed by these studies which are presented in the present paper.

METHODS

A report on the progenies obtained by backcrossing the F_1 *rustica-paniculata* hybrid to *N. rustica* has been made (LAMMERTS 1929). The fertile plants therein described were both selfed and backcrossed. The plants of the backcross were again examined using the usual aceto-carmine technique and those having the highest number of bivalents were selected and backcrossed. By continuing in this way after several backcrosses eleven different lines were obtained from as many parent plants showing $23_{II}+1_I$ at metaphase-I. These cultures were grown in the greenhouse during the winter of 1931 and the chromosome number of about 20 plants in each line was determined. It was found that in general the monosomics (those showing $23_{II}+1_I$ at I–M) were of distinctive morphology, though in some

[1] National Research Fellow.

populations other factors causing variability made the correlation less perfect. In each population a plant most nearly resembling *N. rustica* but having only $23_{II}+1_{I}$ was selected so as to eliminate other possible sources of variation as much as possible. Each was selfed by limited pollination; that is, about 75 to 100 pollen grains were placed on each stigma. As the total number of seeds in a capsule is approximately 500, by pollinating in this way possible competition between n and n−1 grains is eliminated. The same plants were also crossed as female parents to *N. paniculata* (12_{II}), and as male parent to *N. rustica* using the same limited pollination technique as in selfing. Besides two types were crossed as female parents to *N. rustica* in order to see if the proportion of functional n and n−1 female gametes would be comparable to that obtained in the cross to *N. paniculata*. The cultures from these pollinations were grown in the summer of 1931. Classification by morphological characters was not difficult and any doubtful cases were verified by examination of the pollen mother cells.

TABLE 1

Transmission data pertaining to monosomics of N. rustica.

MONOSOMIC TYPE	CROSSED TO *N. paniculata*		USED AS FEMALE PARENT		USED AS MALE PARENT		SELFED	
(DESCRIPTION OF APPEARANCE IN *N. rustica*.)	$12_{II}12_{I}$ HYBRIDS	$12_{II}11_{I}$ HYBRIDS	NORMAL	MONOSOMIC	NORMAL	MONOSOMIC	NORMAL	MONOSOMIC
A. Wide enlarged leaf; thickened stem	59	62	..	..	23	8*	42	70
B. Indistinguishable from normal type	22	69	..	..	104	..	..	..
C. Slightly asymmetrical flower with acute corolla lobes	54 56	27 19	..	..	112 89	1 11	70	47‡
D. Enlarged flower; partially sterile	33	69	38	65	94	..	34	62
E. Acute light green leaf; narrow corolla lobe	16	86	..	..	112 67	.. ..	32 24	41 42
F. Small irregular leaf; flower ruffled	80 75 72	29 32 29	.. .. ..	.. .. ..	85 65 93	39 15 1	60 56 64	33 27 33
G. Rounded dark green cordate leaf; corolla lobes flat	63	53	31	77	104	1	47	52

* Based on observation of morphological differences only.

‡ Also segregating for large leaf type.

THE MONOSOMIC TYPES

Seven of the twelve monosomics that should be obtained theoretically from this hybrid were recovered. These are designated A–G respectively. Data on their inheritance together with a brief description of each is given in table 1. Some idea of the changes in the morphological appearance of the *rustica-paniculata* hybrids brought about by the removal of a single chromosome may be had by reference to figures 1 and 2. These are ex-

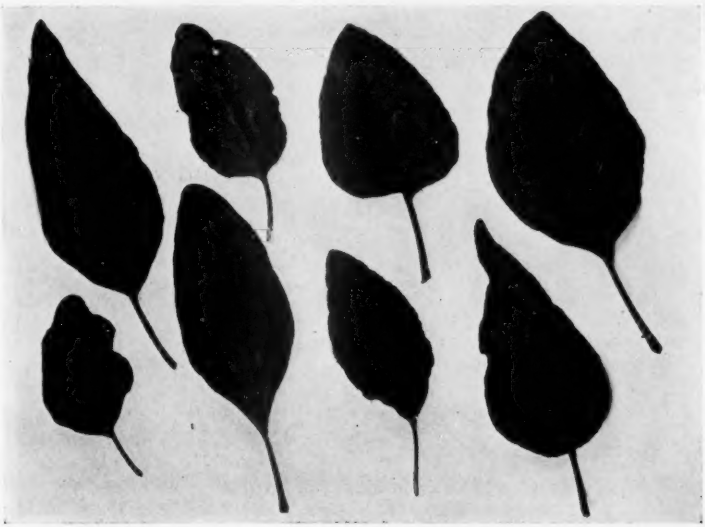

FIGURE 1.—Leaves of the $12_{II}+11_{I}$ *N. rustica-paniculata* hybrids. At bottom left to right are types A–D; top, left to right, E–G, and normal $12_{II}+12_{I}$ hybrid.

amples of the nullosomic condition and the effect is of course less in the monosomics of the corresponding selfed progenies where only one member of the pair is removed. Besides the type recorded in table 1 there were found in each selfed and backcross population from 2 to 7 variants which in certain cases were dwarfs or differed in details of flower morphology. Three unusually luxuriant plants were also found. These variants were selfed and in most cases have given only normal progeny. They were apparently due merely to environmental influences. Some, however, have given progenies exhibiting further variation and these are now being investigated. Although practically all the variants were examined, in no case

were any trisomics found. Only two variants were found in the hybrid populations. One of these appeared in the cross of type A to *N. paniculata*. It was unusually luxuriant and had thick wide leaves with irregular margins. The plant resembled *N. solanifolia* in growth habit but was a true hybrid, the pollen mother cells showing $12_{II}+12_{I}$ at metaphase-I. It was unfortunately as highly sterile as the normal hybrids so that further study could not be made. The lack of variants in the hybrid populations is not clear but may be connected with a slighter sensitivity to environmental influences on the part of the hybrids which were very vigorous.

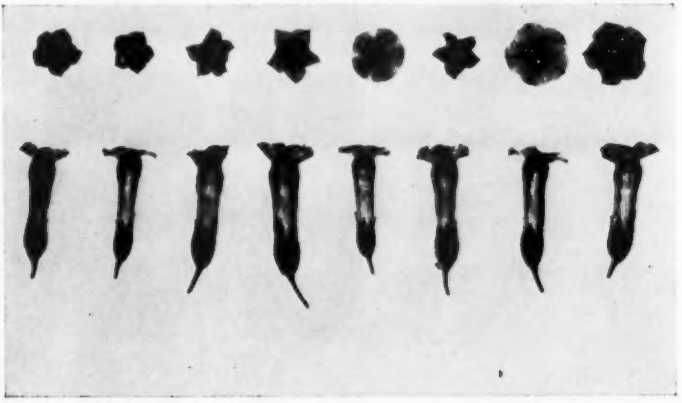

FIGURE 2.—Flowers of $12_{II}+11_{I}$ *N. rustica paniculata* hybrids. From left to right are types A–G and at extreme right the normal $12_{II}+12_{I}$ hybrid. About two-thirds natural size.

Examination of table 1 will show that crosses to *N. paniculata*, backcrosses and selfed progenies were in general comparable as regards the proportion of monosomic plants found. Only in type G do we find differences of possible significance. Here the percentage of nullo-G hybrids is 45 as compared with 71 percent in the female backcross and 52 percent in the selfed lines. This variation probably reflects a great variability in the frequency of lagging of the univalent during the reduction division resulting in varying percentages of micronuclei and $n-1$ gametes. Also in type F where $n-1$ pollen functions occasionally we find a higher proportion of monosomics in selfed lines than in the backcross. Nevertheless for comparative purposes we may class the three populations of a given type together. This has been done in table 2.

It may readily be seen that the monosomics fall into two sharply de-

fined groups consisting of (1) types A, B, D, E, and G in which 56 to 75 percent of the functional gametes are n − 1 and (2) types C and F where only 31 percent are n − 1. The variation in group 1 may well be only a random one although the range is so great as to make it seem likely that the B and E chromosomes lag and accordingly are eliminated much more frequently than A and G with D intermediate in behavior. Direct comparative cytologic study on percentages of lagging as revealed by the number of micronuclei would possibly enable one to decide this question. There can be no doubt however that chromosomes C and F are in a class by themselves. The low percentage of functional n − 1 gametes from these types does not seem to be the result of poor viability. Germination was high (about 95 percent) and the monosomic plants, especially those of

TABLE 2

Functional female gametes from N. rustica monosomics.

MONOSOMIC TYPES	24-CHROMOSOME GAMETES	23-CHROMOSOME GAMETES	TOTAL	PERCENT N-1
A	101	132	233	56
B	22	69	91	75
C	180	83	263	31
D	105	196	301	65
E	90	250	340	73
F	590	183	773	31
G	141	182	323	56

type C, were quite as vigorous as normal plants. Furthermore it is these very types which show an appreciable amount of transmission through the pollen, further evidence that the small number obtained through the female parent probably is not due to a lower viability of these types. It would appear therefore that some other phenomenon is operating to cut down the percentage of functional n − 1 female gametes. Possibilities under investigation are (1) selective development at the four celled stage of megasporogenesis, (2) frequent failure of 2n − 1 zygotes to complete normal seed development, and (3) double division of the univalent involved.

DISCUSSION

One of the most obvious features of the various cultures was that in every case the differences between the monosomics and the normals in *N. rustica* were less pronounced than the corresponding differences in the cultures obtained by crossing the same parent to *N. paniculata*. This was most noticeable in the case of type B which was so similar to the normal

that classification in the selfed progeny was impossible. However, in the hybrid population the nullosomics were readily recognized. The same phenomenon was described by CLAUSEN (1926) in his studies of the fluted and corrugated monosomics of *N. Tabacum*, another Nicotiana species with n=24. Here the regular F_1 *sylvestris-Tabacum* hybrid has 12 *sylvestris* chromosomes paired with 12 *Tabacum* homologs leaving 12 unpaired *Tabacum* chromosomes. The fluted and corrugated hybrids have 12 bivalents and only 11 univalents. In other words these hybrids were nullosomic as regards the fluted and corrugated chromosomes, there being no homologs of them in *N. sylvestris*. Likewise examination of the *rustica-paniculata* hybrids resulting from the union of 23 chromosome gametes and *N. paniculata* pollen showed $12_{II}+11_{I}$ at I-M in each of the seven types. These types were then comparable to those reported by CLAUSEN in *N. Tabacum* and the greater contrast observed in hybrids is because we are here dealing with a nullosomic instead of a monosomic effect. The corresponding condition in *N. rustica* would necessitate the production of plants with both members of a given pair eliminated instead of only one. This has so far proved impossible although every effort has been made including limited self pollination on the shortened style of a type F plant. In no case were any plants exhibiting 23 bivalents at first metaphase-I or extreme development of the monosomic complex found although most of the variants were examined with this idea in mind. Undoubtedly this lack of nullosomics is mainly due to the rarity with which n−1 pollen grains function. It is unnecessary to assume that the nullosomic condition would have a lethal effect although in types F and C such may well be for here we have an appreciable number of n−1 pollen grains functioning. In the case of type F 28 percent of the functional female gametes and 18 percent of the functional male gametes are n−1. Accordingly about 5 percent of nullosomics would be expected. Since none was formed even in progenies resulting from limited pollination on shortened style, one may conclude that the nullosomic has very low viability.

The rather rapid return to the parental chromosome number on the part of the hybrid derivatives obtained by selfing fertile plants in the backcross of F_1 *rustica-paniculata* to *N. rustica* (24_{II}) is therefore mainly due to the infrequency with which pollen grains containing incomplete chromosome sets function.

A study of the comparative effects of removing whole chromosomes in diploid, theoretically amphidiploid and hexaploid species is interesting. BLAKESLEE and BELLING (1924) found that n−1 gametes from a 2n−1 bud variant did not function in *Datura Stramonium*, a diploid species with

n = 12. In *Zea mays*, also a diploid species with n = 10, numerous translocations are being studied by ANDERSON, BURNHAM, and BRINK. As reported by BURNHAM (1930) approximately one-half of the gametes from plants heterozygous for a given translocation are deficient for a section of one chromosome and duplicated as regards the other. In some cases the deficiency is very small and yet such gametes do not function (see BURNHAM [1932]). Monosomics have as yet not been found. In *Oenothera Lamarckiana*, a plant which was 2n − 1/2 gave only normal and 2n + 1/2 plants when self pollinated and crossed to *Oe. Hookeri* (unpublished data of author). Evidently monosomics and deficiencies are not transmitted in diploid species.

N. Tabacum and *N. rustica* are both naturally occurring amphidiploid species having two sets of 12 chromosomes which are to some extent at least homologous though pairing is no longer possible. In both these species monosomics are transmitted readily through the egg but only rarely through the pollen and nullosomics have so far not been obtained.

Finally KIHARA (1924) and NISHIYAMA (1928) report that in *Triticum vulgare* and *spelta* (n = 21) male and female gametes both function and nullosomics having only 20_{II} may be obtained. By crossing monosomics involving different chromosomes plants having $19_{II} + 1_A + 1_B$ were obtained by NISHIYAMA (1928). These when selfed gave among others a few weak plants with only 19_{II}. Recently NISHIYAMA (1931) completed a study of fatuoid oats in *Avena sativa* (n = 21), another supposedly hexaploid species. He found the fatuoid character associated with a certain chromosome, *c*, which may occasionally be eliminated spontaneously. Such a monosomic is transmitted through both ovules and pollen and because of lagging of the univalent only about 1/6 of the gametes are normal. Selfing therefore resulted in 256 homozygous fatuoids (2n = 40), 397 heterozygous fatuoids (2n = 41) and only 42 normals (2n = 42). Here then we have a frequent lagging and no selective elimination of gametes with the incomplete set of chromosomes.

We may therefore conclude from this comparative study that there is a direct relation between the degree of polyploidy and viability of n − 1 gametes and 2n − 2 zygotes. The recovery of monosomics in a supposed diploid species would then be evidence of its polyploid nature. As pointed out by BRIDGES (1921) and CLAUSEN (1926) monosomics may be used advantageously for the determination of linkage groups and also linkage relations within a group. Their use in plants is however limited to amphidiploids and hexaploid species because of their inviability in diploids.

SUMMARY

Seven monosomics in *N. rustica* are described. The percentage of functional n − 1 gametes varies in the individual cases but due to lagging is usually over 50 percent. In two cases, however, only 31 percent of the functional gametes were n − 1. This was not the result of inviability because about 95 percent of the seed germinated and practically all the plants survived. Only three types were transmitted in appreciable frequency through the pollen.

Nullosomic plants (2n − 2) were not obtained even after selfing with a limited amount of pollen on shortened styles.

Hybrid derivatives obtained by selfing fertile plants in the backcross of *N. rustica-paniculata* hybrid to *N. rustica* (24_{II}) return to the chromosome number of *N. rustica* mainly because pollen grains with incomplete chromosome sets rarely function. Zygotes lacking both members of a chromosome pair are probably eliminated even when produced.

Viability of n − 1 gametes and 2n − 2 zygotes is evidence that a species is polyploid.

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INDEX

Page numbers printed in black-faced type refer to headings of articles or of sections. Names in lists of "Literature cited" are not included.

AGOL, I. J., 54
ALTENBURG, E., 655
Amblycorypha, 63
American Association for the Advancement of Science, 29
ANDERSON, E., 177, 178, 197, 199, 235
ANDERSON, E. G., 137, 138, 144, 145, 147, 148, 150, 382, 425, 429, 481, 497, 498, 500, **503**, 504, 695
Angiosperm, 443, 450, 452
Animal improvement, 107
Anlagen complex, 454
Antirrhinum
  glutinosum, 253
  hispanicum, 253
  Ibanyezii, 253
  majus, 176, 179, 253
  molle, 176, 253
  Segovii, 176, 179
  Self-fertility, 253
  Self-sterility, 253
Apple, 265
Arisaema, 453
Arisaema triphyllum, 439, 442
Arrenotoky, 2
Asparagus, 432
  Chromosomes, individuality of, 450
  Crosses, varietal, 436
  Cytological investigations, 443
  davuricus, 436
  Dimorphisms, sexual, 434
  Embryo sac, development of, 449
  Gametophyte, development of female, 448
  Genetic and cytological study, 434
  Hermaphroditism, **438**, 443, 454–456
  Heterotypic division, 444
  Homeotypic division, 446
  Hybridization, **435**, 438, 452, 454
  Megasporogenesis, **448**, 456
  Microsporogenesis, **444**, **447**, 448, 456
  officinalis, **432**, **433**–436, 438, 439, 442, 443, 447, 448, 450, 453–456
    Genetic and cytological investigations on, 432
    History of, 433
    Inheritance, 432
    Variation, 432
  officinalis pseudoscaber, 436
  Reversal of sex, **438**, 439, 442, 443, 452, 456
  Sex determination, mode of, **451**, 453, 455, 456
  Sex intergrades, 438
  Sex ratios, **436**, 452
Asparagus (Continued)
  Variety
    Argenteuil, 433, 436, 446, 447, 456
    Barr's Mammoth, 433, 436, 446, 447, 456
    Bonvallet's Giant, 433, 436, 446, 447, 456
    Columbian Mammoth White, 433
    Conover's Colossal, 433, 443, 446, 447, 456, 462
    Giant Emperor, 433, 436, 446, 447, 456
    Mary Washington, 433, 436, 437, 441–443, 446, 447, 456, 460
    Palmetto, 433, 436, 437, 446, 447, 456, 464
    Purple Dutch, 433
  virgatus, 436
Avena sativa, 695

BABCOCK, E. B., 125, 494
Bacillary white diarrhea, 203
Bacillus pestis caviae, 204
BAGG, H. J., 204, 315, 674–677, 679, 686
Balkeman test, 301
Barley, 121–123
BARLOW, N., 327, 328, 330, 332
Baroid mutation in Drosophila, 369
BARTLETT, H. H., 393, 394, 408, 574
BATESON, W., 181, 452
BAUR, E., 176, 253, 452
Bausch and Lomb oil immersion objective, 650
BEADLE, G. W., 82, 126, 135, 413, 416, 417, 419, 426, 481, 482, 485
BEAN, A. M., 3, 674
BEATUS, R., 234, 273
BELLING, J., 134, 481, 493, 495–497, 573, 661, 694
BENKERT, L. H., 7, 16, 17, 19, 20, 29
BERGEY, D. H., 204
BERNATSKY, J., 432, 435
Bernoulli system, 348
BERNSTEIN, F., 337, 349, 350
BIDDLE, R. L., 153
Biometricians, 108
Bird, 615
BITTER, G., 239
BITTNER, J. J., 468, 478
BLAKEMAN, 301
BLAKESLEE, A. F., 134, 267, 400, 573, 591, 597–599, 694
BLANCHARD, F. C., 393, 394
Blood groups, measuring linkage in human genetics with reference to, 335
BONNER, J., 370
BONNEVIE, K., 675, 676, 686
BONNIER, G., 155

Boothby, W. M., 31
Bostian, C. H., 17, 19
Bostian, N. C., 19, 29
Botanical Garden at Bremen, Germany, 239
Botanical Garden at Triest, Italy, 239
Boycott, A. E., 172
Brandt, A. E., 209, 228
Brassica, 179, 238, 261
  Hybrid, 542
  oleracea, 179, 237, 261
    Self-fertility, 237
    Self-sterility, 237, 261
  oleracea capitata, 178
  pekinensis, 266, 268
  Self-sterility, 261
Bridges, C. B., 60–62, 69–73, 81, 83, 85, 86, 88, 89, 96–99, 137–140, 144, 145, 147–150, 155, 172, 370, 373–375, 381, 382, 386, 497, 637, 647, 695
Brieger, F. G., 178, 193, 194, 232, 235, 237, 262, 266, 634
Brink, R. A., 416, 423, 484, 497, 504, 695
Bristles of hybrids between *Drosophila melanogaster* and *Drosophila simulans*, 153
Brittingham, W. H., 572
Brooklyn Botanic Garden, 239, 637
Brooks, B. W., 261
Brooks, S. L., 42
Buchanan, R. E., 228
Buchholz, J. T., 267
Bucknell University (See University)
Burke, J., 564
Burnham, C. R., 415, 482, 483, 485, 492, 497, 498, 500, 504, 695
Burton, R. H., 6
Bussey Institution, 204
Buxton, B. H., 542

Cabbage, 178
California Institute of Technology, 83, **137**, 153, **369**, **393**, **413**, **481**, 500, **503**, **689**
California, University of (See University)
Camera lucida, 484, 451, 650
Campanula, 133
Cannabis sativa, 439
Capsella, 239, 243, 245, 247–254, 256, 262–264, 267–273
  Bursa grandiflora, 242, 273
  Bursa-pastoris, 239
  Crosses among segregates, 258
  Cross-fertility, 239
  Cross-sterility, 239, **242**, 244, 247, 261
    Backcrosses, 247
    Crosses involving fathers of a common class but different mothers, **251**, 252
    Families from a common mother and different father, 250
    Intra-sterile, inter-fertile groups, **242**, 245–247, 250, 251, 258, 259, 269, 273, 274
    Offspring of reciprocal crosses, **248**, 249
  grandiflora, 176, 239–241, 249, 251, 252, **255**–257, 259, 260, 262, 267, 271, 272, 274, 275, 293, 295
Capsella (Continued)
  Pseudo-fertility, 240, 259, **260**, 261, 263, 264, 273, 275
  rubella, 239–241, 255–258, 260, 272, 274
  Self-fertility, 240, 242, **255**, 257–261, 272, 274, 293, 294
  Self-sterility, 239, 240, **242**, 247, 248, 251, 256–261, 270–275, 294
    Physiology, 265
  Sterility, end-season, 264, 275
  Sterility, proximal, 260
  tuscaloosae, 239–241, 255, 256, 260, 271, 274
  Viguieri, 239, 255, 257, 260, 274
Carcinomata from same gland of mouse, genetic analysis of dissimilar, 468
Card, L. E., 203
Cardamine, 233, 234, 236–238, 243, 269–271, 275
  pratensis, 233, 236, 272, 273
    Self-sterility, 236, 238
  Pseudo-fertility, 234
Carnegie Institution of Washington, 83, 204
Cartledge, J. L., 134
Castle, W. E., 231, 315, 603, 604, 607, 608, 611–615, 617, 686
Cato, 433
Chalmers, R. E., 16, 18
Chamberlain, C. J., 448
Champy, C., 452
Chapman, R. N., 7
Charles, D. R., 31
Cherry, 179, 265
Chicago, University of (See University)
Chicken, 296
Chipman, R. H., 518, 661, 666
Chittenden, R. J., 182
Christoff, M., 511, 518, 622, 625, 631, 632, 636, 661, 666
Chrysanthemum, 133
Cichorium, 233, 261
  Intybus, 239, 242
    Self-fertility, 239
    Self-sterility, 239
Ciona, 265
Clausen, J., 126, 494
Clausen, R. E., 56, 135, 518, 661, 666, 671, 689, 694, 695
Cleland, R. E., 395, 400, 401, 407, **572**, **573**, 577, 579, 589, 591, 593, 596–599
Cloudman, A. M., 468
Cobb, F., 394
Coburn, C. A., 297, 315
Coefficients
  Correlation, 604, 606, 608, 609, 612, 614
  Inbreeding, 228
  Path, 604–611, 614, 615
  Relationships, 228
College of the City of New York, 153
Columbia University (See University)
Comes, O., 512
Compositae, 125
Compton, R. H., 175, 176, 253
Conklin, E. G., **242**

Connecticut Agricultural Experiment Station, 414, **510**, 520, 533
COOPER, D. C., 416, 484, 497
Cornell University (See University)
Correlation coefficient, 108
CORRENS, C., 233–238, 243, 265, 269–273, 275, 432, 434, 435, 452–456
COULTER, J. M., 448
Covariance, 109, 110, 113–116, 118–122
Cow, 296
CRANE, M. B., 179, 265, 548
Crepis, 125, 126, 127, 129, 134
  Aneuploidy in hybrids, 133
  capillaris, 125, 126
  foetida, 125, 129, 133
  grandiflora and self-fertile species, crosses between, 255
  laciniata, 126–128, 130, 134
  leontodontoides, 126, 128
  montana, 126, 127
  mungieri, 126, 127, 134
  rubra, 125, 129, 133
  rubra-foetida, 133
  tectorum, 125
CREW, F. A. E., 452
Cross-fertility, 233, 239, 269
Cross-sterility, **232**, 233, 234, 239, **242**, 244, 247, 261–263, 274, 328, 332

DAHLBERG, G., 560–562, 564, 568, 570
Danysz bacillus, 203
DARLINGTON, C. D., 421, 481, 494–497, 499, 573, 597, 598
DARWIN, C., 233, 332, 454
Datura, 134, 267
Datura Stramonium, 694
DAVENPORT, C. B., 336, 337, 604
DAVIS, B. M., 402–404, 408, 574, 577, 578, 595, 596
DAWSON, W. M., 296
DEMEREC, M., 427
DERMEN, H., 179
Det Norske Videnskapsakademi I Oslo, 64
DE WINTON, D., 147, 148, 177, 178, 197, 199
Digitalis
  ambigua, 542
  Hybrid, 542
  purpurea, 542
Diphtheria, avian, 203
DIVER, C., 172
DOBZHANSKY (See SIVERTZEV-DOBZHANSKY, Mrs. N. P.)
DOBZHANSKY, T., 62, 86, 88, 89, 138, 139, 145, 148–151, 153, **369**, 378–380, 382, 383, 481, 498, 500, 643, 653
DOLAN, L. B., 562
Dominance, 109, **112**–115, 118, 120–123
Dominance bias, effect on progenies, 112
Drosera scheme, 518, 671, 689
Drosophila, 21, **38**, 58, **60**, 63, 74, 75, 77, 81, 82, 97, **137**, 147, 148, 150, 151, 234, 331, 337, 383, 481, 493, 495, 496, 498, 499, **637**, 649, 655, 656

Drosophila (Continued)
  Allelomorphism, 647
    Dilute eye colors, 647
    Tests, 373
  Baroid, description of, 372
  Breeding tests, 40
    With different types of females, 50
  Bristles, **153**, 156–**170**–173
  Character
    Diminished, 61, 62, 66, 69, 70, 72–**78**–80
    Sex-linked, bobbed, 62
  Chiasma formation, 499
  Chromosomal aberrations, 639
  Chromosomal arrangement, 657
  Chromosome, 498
    Association, 482, 498
    Conjugation, 382
  Chromosomes
    Post-diplotene association of, 499
  Coincidence, 89, **96**, **101**, **102**, 104
    Comparison of in normal and inversion-bearing chromosomes, **102**, 104
    Data, analysis of **101**, 102
    Sections located in different arms of the same chromosome, 101
  Crosses
    Preliminary, 158
    Success of, 156
    To test cytoplasmic differences in *melanogaster* stocks, 160
  Crossing over, 481, 482, 498, 499, 644, 645, 652–658
    In one arm, effect of, upon its occurrence in the other, 90
    Values, influence of temperature on, 89, 92, **96**, **98**, 99, 103
  Crossover tests, methods of, 640
  Cytological tests, 55
  Cytology, **637**, 638, 648, 658
    Baroid, 379
    X-radiation induced dominant eye colors, 637
  Deficiency for fourth chromosome recessives, 70
  Disjunction, 498
  Dominance, 371
    Of mutant change present in mosaic, 66
    To recessiveness, change from, 371
  Elimination, somatic, **60**–63, 67, 74, 77
  Eversporting, 38–40, 58, 59
  Gene
    Arc, 154
    Aristaless, 83, 90, 91, 96, 97, 141, 142, 144, 147, 151, 641, 644
    Aristaless-2, 139
    Bar, 160, 171, 369–371, 373, 374, 376, 377, 381–383, 385–388
      Episome, 385, 387
      Protosome, 385–387
    Bar-3, 370
    Bar-4, 370, 373
    Baroid, **369**, 372–374, **375**, **376**, **377**–**379**–**382**–388

Drosophila (Continued)
Gene (Continued)
Baroid (Continued)
Crossing over in the presence of, unequal, 376
Cytology of, 379
Influence of on chromosome conjugation, 382
Translocation associated with, 377
Bent, 55, 70, 72, 73
Black, 69, 70, 77, **78**, 79, 154, 155, 157, 167, 169, 171–173, 379, 381, 641, 644
Black body color, 83–85, 90, 91, 96–98, 101, 139, 147
Bobbed, 154, 384
Bristle, 154, 155
Broad, 39
Brown, 154
Cinnabar, 82, 83, 86, 91, 96–98, 101, 103
Cinnabar-2, 82–85, 88, 90, 92, 96
Claret, 61, 64, 142, 154, 641
Comb, 154
Crossveinless, 39, 155, 371
Curled, 64, 154, 155, 641, 643, 645, 647
Curly, 54, 55, 377, 640, 641, 643, 645–648
Curly wings, 82, 84, 86, 87, 90, 160, 165, 170
Curved, 69, 77, **78**, 79, 154, 169, 641, 642, 645, 654
Curved wings, 139, 141, 145–147
Cut, 39, 371
Cut-6, 155
Deformed, 374
Delta, 171, 172, 647
Dichaete, 640, 641, 645, 647
Discolored, 656
Double-bar, 369, 370, 373, 374, 377, 385
Double-infrabar, 370, 373, 374
Dumpy, 90, 91, 96, 97, 641, 643
Dumpy-2, 643, 644
Dumpy wings, 139, 141, 144
Ebony-4, 154
Echinus, 39, 52–54, 59, 155
Eosin, 58, 637
Eyeless, 57, 70–73, 77, **78**, 80, 371, 372, 640, 645
Eyeless-2, 370, 371
Facet, 39, 48, 52, 53, 56, 59, 171, 377
Forked, 71, 154, 155, 169, 371–376, 386
Fringed, 154
Fused, 154, 372, 376
Gap, 154
Garnet, 155
Garnet-2, 155
Giant, 154, 155
Gray, 38, 39, 48, 58
Hairless, 377, 647
Hairy, 64, 154, 169–171, 641, 643
Infra-bar, 370–374, 386
Lobe, 83–90, 97–99, 101–103, 171, 374
Lozenge, 38, 39, 154, 374
Miniature, 38, 39, 58
Minute, 641, 645–647, 656
Morula, 154
Notched, 39, 41, 42, 46, 48–56, 58, 59
Drosophila (Continued)
Gene (Continued)
Peach, 154, 155
Pink, 70
Plexus, 139, 141, 154, 641, 642, 644, 646–648, 654, 656, 658
Plum, 656
Prickly bristles, 641
Prune, 39, 53, 54, 59, 155
Prune-2, 154
Punch, 655
Purple, 69, 77, **78**, 79, 81, 83–86, 88–91, 96–98, 101–103, 139, 141, 147, 151, 154, 169, 641, 642, 645–647
Recessive kidney, 374
Red, 39, 40, 56
Rough, 154, 171
Roughoid, 64, 69, 142, 154, 641
Ruby, 39, 52–54, 59
Rudimentary, 375, 386
Sable-2, 154
Scarlet, 64, 154, 155, 160, 641, 643, 645, 647
Scute, 39–41, 44, 49, 54, 58, 59, 155
Sepia, 154, 155, 169–171
Singed, 40, 42, 44, 46, 48–51, 54, 55, 58
Small-eye, 386
Small-wing, 155
Sooty, 64, 81, 154, 155, 641
Speck, 83–85, 88, 90, 91, 96, 97, 102, 139, 141, 142, 147, 151, 154, 641, 642, 644, 646–648, 656, 658
Star, 54, 55, 374, 640, 645, 647
Stripe, 64, 154, 155, 641
Tarnished, 656
Thoraxate, 96, 97
Thread, 64, 154, 155, 641, 643
Twisted abdomen, 154
Ultra-bar, 369
Vein, 64, 68
Vermilion, 39, 71, 155, 371, 639
Vestigial, 379, 380, 386, 388
Vestigial wings, 83, 84, 86–88, 90, 91, 96, 97, 99, 101–103
White, 38–40, 48–59, 155
Yellow, 38–41, 44, 46, 48–55, 57–59, 154–156, 371
Genetic and cytological studies on X-radiation induced dominant eye colors of, 637
Genetical analysis of the mosaic female, 66
Genetics, **637**, 638, 642
Gynandromorphs, 61–63
Haploidy for the fourth chromosome in the minute flies derived from the mosaic, cytological demonstration of, 73
Heredity, chromosome theory of, 60
Hybrids, 153
Hyperploid, 40, 42, 44, 46, 48–54, 56, 57, 59
Inheritance, 60, **68**
As a member of the fourth chromosome linkage group, 68
Inversion, 645, 652, 654, 656, 657
Effect of upon temperature effect and coincidence values, 96

Drosophila (Continued)
Lethals, 21
Linkage, **54,** 55
Groups, 68, 640
Translocation, tests for the, 54
melanogaster, 38, **60,** 61, 67, 69, 74, **81, 137,** 151, **153–160,** 162–173, 335, **369,** 370, 648
Chromosome II, 138
Crossing over, 81–85, 90, 103, **138**
Comparison of triploid and diploid for chromosome II, 137
Diploid, **137,** 138, 140–144, 147–151
Triploid, **137, 138**–144, 148, 150, 151
Cytoplasm, effect of, 165
Equational exceptions, **144**–147, 151
Factors suppressing crossing over, 81–85, 90, 103
Inversion, **81,** 82, 86–89, 92, **96,** 98, 99, 101, **102**–104
Somatic elimination of the fourth chromosome in, 60
Triploids, measurement of crossing over, 138
Use of attached-x stocks, 162
Minute, 64–**73,** 74, 77
Mosaic female, occurrence and description of, 64
Mosaic, 62, 63, 65, **66,** 68, **73,** 74, 77
Diminished, 61, 64, 75, 76
Sex, 61
Somatic, 60, 61
Mosaicism, 39, 40, 56, 58, 59
Mottled-eye, **38,** 40–42, 44, 46, 48–59
Due to unstable translocation, 38
Mottled stock, origin of, 38, 39
Mottling, explanation of, 39
Mutant, sex-linked, Minute-n, 62
Mutation, 637, **638,** 640, 641, 647
Eye color
Cream, 637, 639
Dilute, **647,** 648, 656, 658
Dilute-1, 639–642, 644, 648, 650, 653, 657, 658
Dilute-2, 639–642, 644, 648, 650, 653, 654, 657, 658
Dilute-3, 639–642, 644, 650, 657, 658
Dilute-4, 640–642, 645, 650, 654, 657, 658
Dilute-5, 640–642, 645, 650, 654, 657, 658
Dilute-6, 640–642, 645–647, 650, 652, 653, 656–658
Dominant, **637–639**–647, 649, 655, 657
Henna, 639–641, 648–650, 655, 657
Salmon, 639–642, 648, 650, 652, 655–657
Gene, 655
Point, 655, 658
Non-disjunction, 56, 57, 481
Notched wings, 40, 44
Polyploid crossing over, 147
Recessiveness, change from dominance to, 371
Sex ratio, 21

Drosophila (Continued)
simulans, 61, **153,** 155–169, 171–173
Influence of stocks, 167
Synapsis of the chromosomes, 103
Temperature effect, conclusions and discussion of, 98
Theta, 38, 39, 48, 52–54
Translocated fragment, tests for the length of, 52
Translocation, **38**–41, 44, 48, 49, **52, 54,** 55, 58, 59, 145, 149–151, 481, 640, 641, 643–646, 649, 652–658
Associated with baroid, 377
Linkage tests for, 54
Pale, 383, 637, 647, 656, 658
Second chromosome, 378
X-radiation, **637,** 657
Induced dominant eye colors, genetic and cytological studies, 637
Drosophilists, 107
Dubois equation, 31
DUNCAN, 382, 383
DUNN, L. C., 83, 204, 615–617, 681
DURST, C. E., 115

EAST, E. M., 117, 118, **175**–179, 182, 185, 232, 234–236, 238, 244, 245, 251, 253, 255, 256, 261–263, 265, 266, 271, **327,** 330, 332, 333, 413, 511–513, 515, 528, 541–544, 622, 625, 629, 631, 633, 635, 636, 660, 661, 667, 671–673
Ehrlich's haematoxylin, 416, 484
EMERSON, R. A., 31, 117, 118, 360, 414, 415, 425, 427, 429, 482, 485, 500, **503**–505
EMERSON, S. H., **393**–401, 405, 406, 408, 573, 578, 589, 593, 594, 597, 600, 601
ENGLER, A., 433
Eosin, 267
Epilobium, 182
Erythrosin, 267
Euchlaena mexicana, 482
Evolution, 603
EYSTER, L. A., 413
EYSTER, W. H., 413–415, 423

Factor
Environmental, 605
Genetic, 605
FELDMAN, W. M., 31, 33
FERGUSON, M. C., 261
Fertility, **125,** 129, 131–135
In hybrids, pollen grain studies as an indication, 125
FILZER, P., 176, 234–236, 238, 251
FISCH, C., 436
FISHER, R. A., **107,** 108, 112, 207, 210, 220, 606
Fixative
Allen's modification of Bouin's solution, 444, 514, 536, 661
Bouin's solution, 267, 444, 536
Carnoy's solution, 444, 536
Chrom-acetic, 536
Flemming's solution, 73, 74, 536
Flemming's strong solution, 661

Fixative (Continued)
Navaschin's killing agent, 379, 536, 661
Shaffner's chromo-acetic, 444
Flax, 181
FLORIN, R., 233
FLORY, JR., W. S., **432**, **442**, 451, 453
Fly (see Drosophila)
FORTUYN, A. B. D., 111
Fowl, 107, **615**, 616, 618
Analysis of measurements, 615
Character, 615, 618
Size factor, general, 616
Typhoid, 203
White Leghorn, 615, 616, 619
Fragaria, 672
FRATEUR, J., 203
Fritillaria imperialis, 496

GABRITSCHEVSKY, E., 172
GAERTNER, 622
GAIRDNER, A. E., 181
GAISER, L. O., 179
Galton and Mendel Memorial Fund, 38, 153, 231, 296, 510
GARSTANG, S., 172
GATES, R. R., 400, 404
GATES, W. H., 298
Geology, 109
GERHARD, K., 395, 407
GERSHENSON, S. M., 384–386
GILMORE, K. A., 26, 29
GOODSPEED, T. H., 511, 518, 661, 666, 671, 689
Goucher College, 572
GOWEN, 194
GOWEN, J. W., 82, 499
GOWEN, M. S., 82
Graph for standard errors of ratios, 31
Grasshopper, 63
GRAUBARD, M. A., 81
GREEN, C. V., 604
GREGORY, P. W., 604
Growth, heterogonic, **610**, 611, 614, 615
Guinea pigs, 203

Habrobracon, **1**, 2, 21, 22, 24, 28
Antenna of mutant types, 8, **17**, **18**, 28
Binuclearity, egg, 26
Gene
Beaded, **12**, 23, 25, 27, 28
Black eye, 6, 26,
Broad, 14, **20**, 22, 25, 27
Cantaloup, **7**, 23, 24
Confluent, **18**, 19, 22–24, 27
Constricted, **16**, 22, 25, 28
Dahlia, 7, 22, 23, 25, 28
Defective, **2**, 3, 17
Fused, **17**, 22, 23, 25–28
Ivory eye, 6, 7, 17, 22–26, 28, 29
Kidney, **20**, 21, 23, 24
Light, 25, 28
Light ocelli, 22
Long, **17**, 22, 25, 27
Maroon, **7**, 22
Miniature, **13**, 17, 23, 25, 27
Minnesota yellow, **7**, 12

Habrobracon (Continued)
Gene (Continued)
Mosaic black and ivory, 26
Narrow, **16**, 23, 25, 27
Notch, **20**, 22, 25, 26
Orange, 3, **6**, 7, 17, 20, 22, 23, 26, 28, 29
Reduced, **3**, 4, 22, 23, 27
Semilong, **18**, 23, 25, 27
Short, **13**, 16, 27
Shot, **20**, 22, 27
Sooty, 3
Spread, 14, **20**, 22, 25
Stumpy, **12**, 13, 23, 24, 28
Tapering, **19**, 20, 22, 25–28
Truncate, **19**, 23, 24, 27
Twisted, **16**, 23, 25, 28
Vestigial, 14, **19**, 22, 24
Wavy, **16**, 17, 23, 25, 27, 29
Wrinkled, **3**, 22, 25
Yellow, **12**, 23, 24
Genes, contrasted effects of different in corresponding structures, 26
Inheritance, 2
Legs of mutant types, 10
Lethals, 21
Linkage
Genetic tests on, 23
Relations, 2, 22
Male biparentalism, genetic tests on, 23
Mosaicism, 7, 26
Genetic tests on, 23
Mutant, 1–4, 6–8, 10, 12, 13, 16–29
Mosaic, 26
Types, 2–4, 6–8, 10, 12, 13, 16–29
Beaded (legs), **12**, 23, 25, 27, 28
Broad (thorax), 14, **20**, 22, 25, 27
Cantaloup (eyes), **7**, 17, 23, 24
Confluent (wing veins and antennal segments), **18**, 19, 22–24, 27
Constricted (femora), **16**, 22, 25, 28
Dahlia, 7, 22, 23, 25, 28
Defective wing venation, **2**, 3, 17
Deficiency (antennae and posterior extremity), 6
Fused (antennae and tarsi), **17**, 23, 25–28
Kidney (eyes), **20**, 21, 23, 24
Lethal naked pupae, **3**, 22, 25
Long (antennae and wings), **17**, 22, 25, 27
Maroon (eyes), **7**, 22
Miniature (body), **13**, 17, 23, 25, 27
Minnesota yellow (base of antennae), **7**, 12
Narrow (wings), **16**, 23, 25, 27
Notch (wings), **20**, 22, 25, 26
Orange eye and its four allelomorphs, **6**, 23
Reduced (wings and venation), **3**, 22, 23, 27
Semilong (antennae and wings), **18**, 23, 25, 27
Short (wings), **13**, 16, 27
Shot (wing veins), **20**, 22, 27
Small head, **21**, 23, 25

Habrobracon (Continued)
Mutant (Continued)
Types (Continued)
Sooty (mesosternum), 3
Spread (wings), 14, **20**, 22, 25
Stumpy (legs), **12**, 13, 23, 24, 28
Tapering (antennae), **19**, 20, 22, 25–28
Truncate (wing veins and antennal segments), **19**, 23, 24, 27
Twisted (legs), **16**, 23, 25, 28
Unexpanded wings, **19**, 22, 24
Vestigial (wings), 14, **19**, 22, 24
Wavy (wings), **16**, **17**, 23, 25, 27, 29
Wrinkled (wings), **3**, 22, 25
Yellow (base of antennae), **12**, 23, 24
Mutation rate, 21, 28
In mixed stock, 22
In pure stock, 22
In X-rayed material, **22**, 23
Mutation, stage at which occurs, 23
Mutations, 23, 24, 26
Recurrences, 26
Reversions, 26
Sex ratio, 21
Wings of mutant types, 4, **17**, **18**, 22
HAECKER, V., 337
HAGEDOORN, A. L., 203
HAGEDOORN-LABRAND, A. C., 203
HAKANSSON, A., 573, 597
HALDANE, J. B. S., 147, 148
HALL, E. K., 242, 256
HANSON, F. B., 370, 386, 637
Harvard University (See University)
Hemp, 437
HENDERSON, L. J., 31
HERIBERT-NILSSON, N., 253, 574
HERSH, A. H., 372
HERSH, R. K., 372
Hetero-fertilization in maize, 358
Heterosis, 118
HEYER, F., 436
HILL, H. E., 545
HILL, S. E., 239, 274
HIRSCH, N. D. M., 562, 563, 570
HOEPPENER, E., 401, 581, 595, 596
HOLLINGSHEAD, E. L., 125, 126
Hordeum distichum nutans, 121
Hordeum tetrastichum, 121
Horses, 296
HUETTNER, A. F., 75
Humulus, 454
Humulus japonicus, 439
HUSKINS, C. L., 514
HUTCHISON, C. B., 415
HUXLEY, J. S., 603
Hybrid, **125–128**, 129, 132–135
Brassica-Raphanus, 542
Pollen grain studies as an indication of fertility in, 125
Hybrid vigor, 118
Hymenoptera, 22

Illinois, University of (See University)
ILOTT, C., 433
IMMER, F. R., **107**, 409
Inbreeding, 226, 228
Inheritance, sex-linked, 452
Inheritance of wildness and tameness in mice, **296**, **315**
International Congress of Plant Sciences, 256
Iowa State College, 203, 209, **351**, 415
Iron haematoxylin, 73, 74
IRWIN, M. R., 203–205

JANSSENS, F. A., 481, 495, 497
Japanese waltzing mouse, 203
JENKINS, M. T., 415, 422, 427, 504
Jewish Hospital of Brooklyn, 335
JOHANNSEN, 233
John McCormick Institute, 205
JONES, D. F., 413, 414, 429
JONES, H. A., 432–435, 437, 439, 440, 443
JONES, H. E., **560**, 562–564
JORDAN, E. O., 205
JORDAN, H. E., 568
JORGENSEN, C. A., 125
JORGENSON, L. R., 504
JOST, L., 265

KAKIZAKI, Y., 178, 179, 199, 237, 238, 261, 263, 266
KAMO, J., 443
KARPECHENKO, G. D., 542
KAUFMANN, B. P., 494
KELLEY, T. L., 301
KEPPERT, 332
KIHARA, H., 689, 695
KING, R. L., 155
KNIGHT, L. I., 265
KNOX, C. W., 203
KOELREUTER, J. G., 231, 510, 622
KOOS, K., 550
KOSTOFF, D., 625, 660, 661, 666, 670, 671, 673
KRAFKA, J., 372
KRAUS, E. J., 265
KUBANYIA, 336
KUHN, 443
KULKARNI, C. G., 394, 577
KUWADA, Y., 494

LAMBERT, W. V., 203, 228
LAMMERTS, W. E., 129, 133, 518, 537, 540, 543, **689**
LANCEFIELD, D. E., 83
LANDSTEINER, K., 336–338, 341, 342, 349
LANGENDORF, J., 400, 402, 407
LAUTERBACH, C. E., 561, 566, 568, 570
LAWRENCE, W. J. C., 179, 236, 237, 255, 272
Leber's disease, 336
LEHMANN, E., 176, 182, 235, 236, 238
LESLEY, J. W., **545**, 547, 550, 551, 554, 556
LESLEY, M. M., 546, 551
Lettuce, 115, 123
LEVINE, P., 336–338, 341, 342, 349
LEVITSKY, 432
LEWIS, P. A., 203
Lexian ratio, 211, 228

Lilium, 261
Self-sterility, 261
Limnaea, 172
Linaria vulgaris, 236
LINDSAY, R. H., 443, 450, 452
LINDSTROM, E. W., 120, 228, **351**, 353–355, 550, 554, 556, 558
Linkage, **335**–338, 346, 349, 350, 353
In human genetics
Agglutinogens, **337**, 349
Derivation of Q, 346
Derivation of standard error, 347
Measuring with reference to blood groups, 335
Relations of genes in Oenothera, 393
Linum usitatissimum, 181
LITTLE, C. C., 204, 468, 469, 478, **674**, 682, 687
LOCKHART, L. P., 205, 213
Louisiana State University (See University)
LUCE, W. M., 373
LUSH, J. L., 228
LYNCH, C. J., 172, 204
Lythrum, 327, 328
Lythrum salicaria, **327**, 330, 333
Cross-sterility, 328, 332
Heterostyly, 327, 328
Lethals, balanced, 331–333
Mutation, 331–333
Non-disjunction, 331
Self-sterility, 328, 332

MACARTHUR, J. W., 352, 353, 545
MCCLINTOCK, B., 363, 416, 421, 482–484, 486–488, 493, 497, 498, 500, 545
MCCRAY, F. A., **621**, 625, **660**
MACDOWELL, E. C., 204, 603, 607, 608, 614, 615
MCPHEE, H. C., 437, 439
MCPHETERS, B. W., 674
MADLENER, M., 336
MAEKAWA, 453
Magenta, 267
Maine, University of (See University)
Maize, 58, 82, 117, 118, 120, 122, 123, 126, **358**, 359, 366, 367, **413**, 414, 419, 421, 422, 482, 483–490, 492–494, 497–500, **503**–505
Allelomorphs, **503**, **504**, **505**, 508
Character, silkless, 429
Chromosome, map of, 483
Crossing over between teosinte and, 484
Cross-sterility, 413
Embryo sac
Lilium type, 358, 362
Smilacina type, 362
Endosperm chimeras, 58
Fertilization, 358
Gametogenesis, 358
Gene
Brown midrib, 415
Chocolate pericarp, 425
Color
Aleurone, 423, 482, 503–506, 508, 509
Pericarp, 503–509
Plant, 503–509
Silk, 503, 505, 507–509
Maize (Continued)
Gene (Continued)
Crinkly leaves, 423
Dwarf, 423
Iojap stripe, 415
Male sterile, 413–415, 422–427–430
Purple plant color, 422
Shrunken endosperm, 423, 482
Slit leaf blade, 426
Tassel seed, 423
Variable sterile, **414**, 416, **417**, 419, 421, 428, 430
Cytological observations, 417
Description, 416
Inheritance, 416
Virescent seedling, 482
Warty anthers, **414**, 421, **422**, 429, 430
Waxy endosperm, 423, 482
Yellow endosperm, 422
Yellow green, 482
Genes
Pollen sterility, 413
Relation to pigmentation, 503
Hetero-fertilization, **358**, **359**–**361**–**367**, 368
Extent of, 367
Genetic tests of the nature of, 361
Megaspores, persistence of the four, 362
Mutation, 362
Non-disjunction, 363
Sperms from two pollen grains, 366
Hybrids between teosinte and, 489
Inheritance
Of a quantitative character, 117
Of scutellum color, 359
Linkage, 425, 426
Mutation, 358, **362**, 363
Non-disjunction, 358, **363**, 365, 368
Phenomenon of hetero-fertilization, 359
Pigmentation, **503**–505
Pollen development, normal, 416
Pollen sterile characters, intercrosses of, 427
Pollen sterility, **413**, 414, 422, 425–**427**, 430
Self-sterility, 413
Translocation, 483, 487, 489, 495, 497, 498, 500, 695
Variety
Alberta flint, 415
Argentine flint, 415
Cornell-11, 415
Missouri dent, 117
Onondaga White Dent, 505, 507
Tom Thumb pop, 117
MALHOTRA, R. C., 437, 438
Man, 335, 336, **561**, 569, 604
Character
Atopic hypersensitiveness, 336
Brachydactyly, 337
Lobster claw, 337
Polydactylism, 335–337
Sex-linked
Haemophilia, 336
Night-blindness, 336
Optic atrophy, 336
Red-green color-blindness, 336
Telangiectasis, 336

Man (Continued)
Character (Continued)
White forelock, 335
Zygodactyly, 337
Left-handedness in twins, 560
Linkage, 335–338, 346, 349, 350
Twin, classification of type, 564
Twins, **560,** 563
Asymmetry, **564,** 567, 570
Character
Ambidexterity, 562
Crown, double, 565, 567
Crown whorl, 565
Dextro-sinistrality, 565
Left-eyedness, 565, 566
Left-handedness, 560–562, 565, 568–570
Right-eyedness, 565
Right-handedness, 562
Sinistrality, 568
Dizygotic, 561, 566, 568, 569
Fraternal, 561–566, 568–570
Identical, 560, 562–566, 568–570
Mirror reversal, 560, 569
Monozygotic, 560, 561, 566, 568, 569
Reversed asymmetry, 561, 568
Sampling, method of, 563
MANGELSDORF, A. J., 176, 193, 194, 234–236, 244, 245, 251, 253, 262
Marine Biological Laboratory, 29, 137
MAY, H. G., 369
Melandrium album, 437
Memorial Hospital, New York, 204
Mendelian factors, 108
Mendelian ratio, 258, 311
Mendelian scheme, 107
Mendelizing system, 110
Mercurialis, 453
Mercurialis annua, 436, 439
METZ, C. W., 155
MEYERS, M. T., 503, 504
Microscope
Spencer binocular, 648
Zeiss, 460
MILLER, E. C., 358
MJOEN, J. H., 604
MOHR, O. L., 52, **60,** 64, 72, 75, 80, 171
MORGAN, L. V., 60, 62, 145, 155, 370, 497
MORGAN, T. H., 61, 62, 81, 86, 88, 89, 97, 98, 145, 149, 153, 155, 156, 171, 172, 265, 335, 369, 375, 382, 386
Morus alba, 439
Mouse, 111, 123, **203**–205, 218, 219, 227, **296**–302, 306, 310, 312–316, 325, **468,** 469, 474, 476, 477, 479, 604, **674,** 677, 687
Abnormality
Genetics of in descendants of X-rayed, 674
Inherited, 674
Age factor in resistance to *Salmonella aertrycke*, 219
Backcrosses, 306
Cancer, 478
Character, 675

Mouse (Continued)
Character (Continued)
Abnormality
Eye, 674, 675, 679–682, 686, 687
Foot, 685
Genetics, 677
Limb, 674–681, **685, 686,** 687
Brachydactyly, 674
Polydactyly, 674, 675
Short ear, 603
Syndactyly, 674
Tameness, **296,** 297, 306, 309, 315, 316, 324
White forehead, 681
Wildness, **296,** 297, 306, 309, 315, 316, 318, 324–326
Factors, estimation of the number of genetic, 310
Gene
Agouti, 316, 325, 326, 684, 685
Albinism, 310, 316, 325, 326, 468, 684, 685, 687
Black, 684, 685
Brown, 310, 316, 325, 326, 468, 604, 684–687
Color, 468
Dilute, 468, 687
Hemorrhagic lesion, 675, 676
Intensity, 468, 684
Myencephalic blebs, 676, 686
Non-agouti, 310, 468
Piebald, 468
Pink eye, 310, 316, 325, 326
Self color, 468
Short ear, 310, 316, 325
Inbreeding, **220,** 226, 228
Inheritance
Degrees of learning, 315
Reaction time, 315
Resistance to *Salmonella aertrycke* in various strains, 203
Wildness and tameness, **296,** 315
Linkage, **310,** 325, 326, 604, **684,** 685, 687
Mammary gland
Carcinomata, 469
Tumors, 468, 478, 479
Out-cross experiment, 682
Parental strains, 302
Runway test, **298, 301,** 302
Salmonella aertrycke, results of selection for resistance, 213
Selection
And mating of breeding stock, 300
In the wild and tame stocks, 307
Influence of individuals in, 223
Sex factor in resistance to *Salmonella aertrycke*, 219
Size factor, group, 604
Strain
Albino, 297, 301, 303–305, 318, 320, 321
Bagg albino, 204, 208, 227, 468
Dilute-brown, 204, 227
English silver, 204, 227
Little dilute-brown, 204, 227
Piebald, 204

Mouse (Continued)
Strain (Continued)
Pink-eyed, 204
Pink-eyed brown, 298, 318
Pink-eyed short eared brown, 298, **303**, 318
Schwing albino, 204, 206–210, 227
Short-eared, 204, 227
Strong dark-brown, 204, 208, 227
White-faced, 204, 227
Tailrings in, 111, 123
Tame, **297**, 300–**307**, 308–324, 326
Tumor, 472–474, 476–479
Differences, physiological and genetic, 479
Transplantation, 478, 479
Weight factor in resistance to *Salmonella aertrycke*, 219
Wild, **297**, 298, 300, 301, 303–**307**, 308–322, 324
X-rayed, genetics of abnormalities appearing in the descendants of, 674
MULLER, H. J., 54, 57, 80–82, 145, 149, 370, 375, 378, 383, 384, 637, 641, 653, 655, 656
MURRAY, W. S., 676, 679, 682, 687
Mus bactrianus, 604
Mus musculus, 111, 204, 468, 604
Mus wagneri, 111
Mutants in Habrobracon, 1–4, 6–8, 10, 12, 13, 16–29

NAKAMURA, T., 432, 435, 439, 443
NAMIKAWA, I., 265
National Academy of Sciences, 572
National Research Council, 29, 107, 572
NEALL, H. E., 565
NEWMAN, H. H., 560–562, 564, 566, 568, 570
NEWTON, W. C. F., 542
Nicotiana, 128, 129, 135, 234, 235, 237, 244, 249, 253, 255, 256, 261, 262, 265, 266, 268–271, 516, 542, 543, **621**, 631–633, **660**, **689**, 694
acuminata, 623, 625, 632, 662
alata, 175–177, 197, 199, 201, 261, 622, 623, 632, 633, 636, 660, 662
attenuata, 632
Bigelovii, 622–625, 628, 629, 631, 632, 634–636
caudigera, 623, 625, 632, 662
Cavanillesii, 622, 623, 632
Character, 672
Flower, 664, 690
Leaf, 664, 690
Stem, 664
Compatibility of species, **621**, 633–635
Cross-sterility, 234
Forgetiana, 175, 201, 261
Gametes, functional, 537
Gametogenesis, 670
Gene, ivory, 193
glauca, 622–632, 634–636, 660, 662, 672
glutinosa, 622–625, 629–632, 634–636, 660, 662, 672
glutinosa tomentosa, 624
Hybrid, 515–518, 525, 527, 540, 621, 622, 625, 629, 631–635, **660**, 691, 692, 694, 696
Tetraploid, **510**, 511, 526, 528, 533–543

Nicotiana (Continued)
Hybrid (Continued)
Triple species, **660**–673
Inheritance
Anther color and pollen color, **196**, 197, 200
Color factors, 193
Corolla color, **193**, 194, 200
Green *versus* non-green corolla, 198
Langsdorffii, 175–**179**, **180**–**182**–**184**–186, 189–**192**–194, 196–201, 253, 621, 623–626, 632, 634, 636, 660–672
Self-fertility, 253, 255
Self-sterility, 253, 255, 256
longiflora, 622, 632, 634, 662
Megasporogenesis, 667, 693
Monosomics, **689**, **691**–696
nudicaulis, 622–625, 628, 630, 632, 634–636, 662
Nullosomics, 694–696
Palmeri, 622–624, 626–629, 631, 632, 634–636, 662
paniculata, 129, 133, **510**, 511, 513–517, 519, 520, 522, 524–531, 535–538, 541–543, 621–623, 630, 632, 633, 636, 660, 661, 663–672, 689–694, 696
Histology of ovaries of tetraploid plants following pollination, 536
Petunioides, 633
plumbaginifolia, 622–626, 629, 631, 632, 634, 635, 662
Pseudo-fertility, 235, 261
Rusbyi, 622–628, 632, 634–636, 660, 662, 671, 672
rustica, 129, 133, **510**, 511, 515, 517, 522, 525–529, 542, 543, 622, 632, 633, 660–673, **689**–696
Inheritance of monosomics, 689
rustica brasilia, 528
rustica humilis, 511–513, 528, 529, 621–623, 625, 661, 663
rustica-paniculata, 133, 540
rustica pumila, 511–514, 516–520, 524, 529, 531, 535, 537, 538, 541–543, 623
Sanderae, 175, 176, **179**, **180**–**182**–**184**–**192**–194, 196–201, 262, 622, 623, 632, 660, 662, 671, 672
Self-fertility, 235, 262
Self-sterility, 234, 235, 253, 255, 256, 261, 262
solanifolia, 692
suaveolens, 622–625, 627–629, 632, 634, 636, 662
sylvestris, 623–625, 631, 632, 634, 660, 671, 672, 694
Tabacum, 625, 632–634, 636, 660, 662, 671, 672, 689, 694, 695
Tabacum angustifolia, 623, 625, 631, 662
Tabacum macrophylla, 622–624, 629, 630, 634, 635, 662
Tabacum purpurea, 623, 625, 662
Tabacum sanguinea, 660
Tetraploid hybrids, cytogenetic behavior, 510

Nicotiana (Continued)
tomentosa, 622–625, 627, 630, 632, 634–636, 660, 662, 671, 672
trigonophylla, 622–624, 629, 631, 632, 634–636, 662
NISHIYAMA, I., 689, 695
Nomography, 31, 33, 34
NORTON, J. B., 432, 433, 435, 436, 439

OCCAM, 331
ODELL, C. W., 301
OEHLKERS, F., 395, 401, 407, 573, 589, 593, 596
Oenothera, 135, **393**, 401, 410, **572**, 589, 593, 596–598, 600, 601
accelerans, 398, 399
acuens, 401, 596, 597, 599
albata, 576
albicans, 394, 400, 401, 403–407, 586, 595, 599
biennis, 400–404, 407, 592
biennis-Chicago, 393
Character, 575–579, 581–588, 590–593
Buds, 594
Flower color, 594
Flower size, 393, 595–597, 600
Foliage, 594
Habit, 594
Stem, 594
chicagoensis, 393
Chromosome cohesion, 573, **589**, 590, 594, **597, 600**
Circle formation, **572**, 573, 575–580, 582, 584, 586–592, 595, 596, 599, 601
Cockerelli, 404
curtans, 404, 407
curvans, 394, 395, 404, 575, 576, 582–584, 590–592, 599
densa, 393
elongans, 404
excellens, 393, 394, 599
flava, 590–592
flavens, 394–396, 398, 405–407, 411, 576, 585, 586, 588, 591, 592, 599
flectens, 394
Flower size, 400, 404
franciscana, 395–397, 399, 400, 402–406, 410, 574, 577–588, 593, 595–599
franciscana sulfurea, 405, 406
gaudens, 393–396, 401, 404, 407–409, 587, 591, 595, 599
Gene
brevistylis, 393, **407**, 409, 410
Broad leaves, 394
bullata, 396
Curved stems, 394
Double flowers, 396
Dwarf stature, 395, 398, 400, 405, 410
Flower size, large, 401, 407
Flower size, small, 400, 401, 405, 406, 408, 410
Green buds with no punctation on the stems, 397
Green buds with punctate stems, 397
Long styles, 408–410
Marginate leaves, 394
nanella stature, 393, 395, 410
Old-gold flower color, 395, 410
Pointed buds and leaves, 394
Punctate stems, 394, 397, 410
Red mid-ribs, 394, 395, 407, 408, 410
Revolute leaves, 398, 408
rubricalyx bud color with punctate stems, 397
Striped bud color, 395, 406
Striped bud cones with punctate stems, 397, 405
Sulfur flower color, 395, 397, 405, 410
White mid-ribs, 408
Yellow flower color, 397
grandiflora, 403, 574, 579, 593, 596, 600
Hookeri, 395, 396, 400–402, 404, 407, 574–576, 578, 580–585, 587, 589–592, 595–600, 695
Hookeri-curva, 590–592
Hybrid, 573, 578, 589–600
Inheritance
brevistylis, 407
Flower size, 401, 411
jugens, 395, 398, 399, 408, 409
laeta, 586, 587, 591
Lamarckiana, 393–396, 401, 404, 407–410, 574, 586–588, 590–592, 600, 695
Lamarckiana brevistylis, 407, 408
Lamarckiana nanella, 393
latifrons, 395, 397–399
laxa, 394
Linkage, 393–**395**, **396**, **398**, **399**, **408**–411, 573, 589, 597, 600
Between chromosomes, 398
Between flower size and *brevistylis*, **408**–410
Relations of dwarf stature, 399
Relations of genes, 393
Relationships, variable, 393
Within chromosome, 395, 396
lutescens, 398
muricata, 401, 404, 574–576, 581, 582, 589–592, 600
pratincola, 394, 408
punctulans, 599
purpurata, 401
rigens, 401, 404, 407, 574–576, 582, 583, 589–592, 599
rubens, 394, 395, 401, 402, 404, 592, 596, 599
rubricalyx, 395, 404
Segmental interchange, 573, 574, 578, 598, 600, 601
Shulliana, 408, 409
suaveolens, 405, 406, 574, 576, 584, 585, 590–592, 600
sulfurens, 395, 399, 405, 406
truncans, 401, 596, 597, 599
truncata, 596
velans, 394–399, 401, 404, 406–408, 587, 588, 592, 595, 599
velutina, 401, 407, 586–588

Ogura, S., 384
Ojemann, R. H., 562
Oliver, 436
Oliver, C. P., 638, 655, 656

Painter, T. S., 55, 57, 145, 149, 151, 378, 653, 656
Paratyphoid-enteritidis, 204, 213
Park, J. B., 177, 235, 238, 244, 261, 265, 266
Parsons, B. S., 566
Patterson, J. T., **38**, 56, 80, 656
Payne, F., 82, 89
Pears, 233
Pearson, K., frontispiece, xi, 31
Pearson, N. E., 63
Pearsonian curves, 110
Pellew, C., 182
Pennsylvania, University of (See University)
Peromyscus maniculatus, 604
Petroff-Hausser bacteria counter, 205
Petunia, 261
Petunia violacea, 176, 179
Physiological salt solution, 205, 648
Physiology, gene action, 603
Pittsburgh, University of (See University)
Plant improvement, 107
Plants
  Cross-sterility in, **232**–234, **242**, 244, 247, 261–263, 274
  Inheritance of height of, 118
  Self-sterility in, **232**-**242**, 247, 248, 251, **253**, 255–262, 265, 266, 268, 270, 272–275, 294, 295
Plough, H. H., 88
Plums, 179, 265
Pollen grain studies an indication of fertility in hybrids, 125
Pollen sterility, genes in maize for, 413
Pollen studies in hybrids, 128
Pollen studies in pure species, 126
Poole, C. F., 125
Poultry, 203
Prantl, K., 433
Prell, H., 234, 236, 251
Primula, 147, 148
Primula sinensis, 147
Princeton University (See University)
Pritchard, F. G., 439
Pritchett, I. L., 203, 213
Pseudo-fertility, 234, 235, 240, 259, **260**–264, 273, 275
Public Health Laboratory, Manchester, England, 205

Quantitative characters, 107, 108, 117
Quantitative inheritance, **107**, 117, 118, 121, 123
  Genetical interpretation of statistics of third degree, 107
Quelprud, T., 74
Quinan, C., 565

Rabbit, 603, 604, 607–609, 611–619
  Character, 607–612, 614, 615, 618
  Linkage, 604
Rabbit (Continued)
  Population, analysis of, 607
  Race
    Flemish Giant, 611–613, 615
    Polish, 611–613, 615
  Sex differences, 615
Radium, 434
Randolph, L. F., 416, 429
Rankin, D., 572
Raphanus sativus, 542
Rat, 203, 686
Ratios, graph for standard errors of, 31
Redfield, H., **137**, 138, 140–142, 144, 147–150, 172, 497, 498, 500, 647
Reitz, H. L., 301
Renner, O., 393–395, 397, 398, 400, 401, 404, 406, 407, 410, 572, 574–576, 581, 584, 589–592, 595–597
Reseda odorata, 175, 253
  Self-fertility, 253
  Self-sterility, 253
Rhoades, M. M., 414, 497
Richey, F. D., 360, 505
Riddle, O., 438, 452
Ridgeway, H. W., 433
Riley, H. P., **231**, 242, 256
Robbins, W. W., 432–435, 437, 439, 440, 443
Roberts, E., 203, 296–298
Rockefeller Institute for Medical Research, **203**, 204
Roscoe B. Jackson Memorial Laboratory, 468, 674
Rothamsted Experimental Station, **107**, 121
Rudloff, F., 401
Rye, 253
  Self-fertility, 253
  Self-sterility, 253

Sachs-Skalinska, M., 193
Sadovnikova-Koltzova, M. P., 315
Salmonella aertrycke, **203**–209, 211–213, 227
  Immunity in mice, **218**, 219
  Reactions under the standard dose in mice, 209
  Results of selection for resistance to in mice, 213
  Standardization of dosage in mice, 205
  Virulence of the organism, 212
Sandiford, R. B., 31
Sands, H., 494
Savage, W. G., 205
Sax, K., 481, 493, 495, 497, 498
Saxifrage, 268
Schaffner, J. H., 439, 442, 452, 453
Schleicher, 33
Schott, R. G., 203
Schuell, 33
Schultz, J., 83, 374, 494, 500
Schwemmle, G., 182
Schwing, E., 204
Self-fertile plants
  Behavior of crosses between self-sterile and, 175
  Relations between self-sterile and, 253

Self-fertility, **175**–178, 180, 183–185, 187–190, 193, 195, 199, 232, 235, 239, 240, 242, **253**, **255**–262, 267, 270–275, 293, 294
Self sterile plants
Behavior of crosses between self-fertile and, 175
Relations between self-fertile and, 253
Self-sterility, **175**–179, 182, 183, 185, 190, 195, 199, 200, **231**, **232**–240, **242**, 247, 248, 251, **253**, 255–262, 265, 266, 268, 270–275, 294, 295, 328, 332
Cardamine-Typus, 238
Cruciferae type, 238
Inheritance of
Cruciferen-Typus, 237
Personaten-Typus, 237
Saxifragaceen-Typus, 237
Tubifloren-Typus, 237
Shepherd's Purse, **231**, **242**, 247, 248, 251, 256–261, 270–275, 294, 295
Studies on, 175
SENN, P. H., 423
SEREBROVSKY, A. S., 54
SETCHELL, W. A., 512, 513
Sex determination in dioecious seed plants, Realizators, 452–456
SEYSTER, E. W., 372
Sheep, character, short ear, 603
SHEN, E., 301
Shepherd's Purse, **231**, 253, 256, 263, 267, 270
Self-sterility in, **231**, **242**, 247, 248, 251, 256–261, 270–275, 294, 295
SHEPPARD, 612
SHLAER, 88
SHOJI, T., 432, 435, 439, 443
SHULL, G. H., 135, 176, 239, 240, 242, 243, 248, 255, 256, 258, 260, 393, 395–398, 407, 408, 410, 452, 572, 574, 577, 579
SIEMENS, H. W., 561, 564, 570
Silene roemeri, 454
SINGLETON, W. R., 413, 414, **510**, 541, 670
SIRKS, M. J., 176, 178, 233, 234, 236, 237, 244, 255, 261, 270
SIVERTZEV-DOBZHANSKY, Mrs. N. P., 370
Size factors, **603**, 605
General, **603**–608, 610, 611, 614, 616–619
Group, **603**–606, 609–611, 617–619
Special, **603**–606, 610, 611, 617–619
SMITH, F. F., 261, 266
SNEDECOR, G. W., 209, 228
SNYDER, L., 336
SÖMME, S., 147
Solanum luteum, 125
Solanum nigrum, 125
Spearman Brown formula, 301
Spinacia, 454
SPRAGUE, G. F., **358**, 359, 414, 486
STADLER, L. J., 58, 362, 483
Stain
Aceto-carmine, 415, 483, 484, 514, 515, 689
Belling's iron-aceto carmine, 126, 661
Crystal violet, 514
Delafield's haematoxylin, 267
Ehrlich's haematoxylin, 416, 484
Stain (Continued)
Eosin, 648
Gentian violet, 661
Haidenhain's iron-alum haematoxylin, 73, 74, 444, 514, 648, 661
Newton's gentian violet, 514
Safranin, 267
White's magdala red, safranin, azure II, 444
Standard error, **31**–33, 111, 116, 117, 121, 123, 124
Standard errors of ratios, graph for, 31
Station for Experimental Evolution, 239
Statistics of the second degree, 110
Statistics of the third degree, **107**, 109, 110, 114, 120, 122
Quantitative inheritance, genetical interpretation, 107
STERN, C., 62, 88, 145, 370, 384
Stizolobium, 134
STOCKARD, 561
STOUT, A. B., 233, 238, 239, 242, 245, 253, 261, 265, 268, 413
STRASBURGER, E., 437, 439
STRONG, L. C., 204, 468, 469, 472, 478
STURTEVANT, A. H., 61, 75, 81–83, 86–89, 97, 98, 145, 149, 153, 155, 156, 160, 161, 167, 169, 171, 172, 369, 370, 375–377, 379, 382, 384–386, 388, 393–401, 405–409, 493, 497, 498, 500, 578, 600, 601
STURTEVANT, E. L., 433
SUMNER, F. B., 604
Superdominance, 123

Tameness in mice, inheritance of wildness and, **296**, 315
TEDIN, O., **107**, 121
Teosinte, **486**, 487, 489, 492, 493, 496–500
Crossing over, 483
Crossing over between maize and, 484
Durango form, 482, 483, 485–492, 499
Florida form, 482, 483, 485–488, 490, 491, 493, 499
TERAO, H., 176, 179
Texas, University of (See University)
Thalictrum dasycarpum, 439
Thalictrum dioicum, 439
THOMPSON, D. H., 385, 386
TICE, S. C., 369, 385
TISCHLER, G., 443
Tobacco, 56
Variegation, carmine-coral, 56
TOLMAN, E. C., 315
Tolmiea, 237, 268
Tolmiea Menziesii, 233
Cross-fertility, 233
Self-sterility, 233
Tomato, **351**, 353–355, 357, **545**, 549, 553, 555, 558
Frist-chromosome genes in the, 351
Fruit-size relations with the, 354
Linear order of, 352
Fruit shape, 558
Gene, 545

Tomato (Continued)
Gene (Continued)
Compound inflorescence, 351, 354–357, 548
Cut leaf form, 555
Dwarf, 551–553, 555, 556, 558
Dwarf growth habit, 351, 354
Fruit size, 558, 559
Inflorescence, manifold effects of the, 355
Lutescent foliage and stigma color, 553–555
Non-purple stem, 555
Non-yellow, 555
Normal green foliage and stigma color, 553–555
Oblate major fruit shape, 351
Ovate major fruit shape, 351, 354
Potato leaf form, 555
Pubescent epidermis, 351
Purple stem, 555
Red flesh color, 552, 553, 555
Simple inflorescence, 351, 356, 548
Skin color of fruits, 555
Smooth epidermis, 351
Standard, 552, 553, 555, 556, 558
Tall growth habit, 351
Yellow flesh color, 552–555, 558
Genes
First chromosome, 351
Fruit size relations with the first-chromosome, 354
Linear order of first-chromosome, 352
Growth habit, 558
Hybrids, 551, 557
Inheritance
Disomic, 554, 555, 557
Trisomic, **551**–553
Linkage, 353, 554, 558
Non-hybrid, 546, 547
Simple-trisomic types, **546**, 548–550, 557, 558
Tetrasomic types, **546**, 550, 551
Trisomic types, **545**–547, 549, 552–**554**
Characteristics of, 554
Variety
Dwarf Aristocrat, 546, 547, 549, 552–554, 556, 558
Dwarf Champion, 553
Grape Cluster, 355, 356
Marglobe, 351, 354
Red Pear, 556
TOPLEY, W. W. C., 205
TORVIK, M. M., 7, 20
Tradescantia, 494
Translocation, a new type of mottled-eyed Drosophila due to an unstable, 38
Triticum, 689
Triticum spelta, 695
Triticum vulgare, 695
Tuberculosis, 203
TURNER, F. M., 172
Typhoid, mouse, 204, 205
TYZZER, E. E., 203, 469

UBISCH, VON, G., 327, 330, 332
UMANSKI, A. J. V., 31
United States Department of Agriculture, **358**, 360, 414, 415
University
Bucknell, 415
Columbia, **31**, **81**, 83, 204
Cornell, 360, 413–415, 500, **503**
Harvard, **175**, **327**, 510, **621**, **660**
Louisiana State, 298
Oslo, Anatomical Institute, 60
Princeton, **231**, 239, 242, 273
Washington, 637
University of
California, **125**, 511, 545, **560**
Chicago, 29, 603
Illinois, **296**, 297
Maine, 204
Pennsylvania, 579
Pittsburgh, **1**, 29
Texas, 38
Virginia, 432
Wisconsin, 204

VAISBERG, M., 342, 343
VAN ATTA, E. A., 637
VAN ATTA, E. W., 639
VAN ATTA, L. C., 639
Variance, 108–110, 112, 113, 116–119
Analysis of, **617**, 618
Vaughan's Seed Store, 433
Veal infusion agar slants, 205
Verbascum, 179, 256
Verbascum phoeniceum, 176, 179, 233, 236, 237, 261
Verbascum, self-sterility, 256
Veronica, 256, 269
Self-sterility, 256
syriaca, 176, 234, 235
Cross-sterility, 234
Self-sterility, 234, 235
VERSCHUER, VON O., 561, 566, 570
VICARI, E. M., 315
Victoreen dosimeter, 638
Virginia, University of (See University)
VRIES, DE, H., 393, 394, 401, 402, 407, 408, 572, **574**, 595, 596

WALSH, L. B., 261
WARD, L., 82
Washington University (See University)
Wasp, parasitic (See Habrobracon)
WATKINS, A. E., 689
WEATHERWAX, P., 358
WEBSTER, L. T., 204, 213
Weibullsholm Plant Breeding Station, 107
WEINSTEIN, A., 89, 637
WEITZ, W., 560
WELDIN, J. C., 204
WENSTRUP, E. J., 6
WERKMAN, C. H., 228
WHITE, O. E., 444, 457
WHITING, A. R., 6, 12, 18, 20
WHITING, P. W., **1**, 3, 6, 7, 13, 17, 21, 26

WHITMAN, 438
WIENER, A. S., **335**, 342, 343
WIGGANS, R. G., 415
Wildness and tameness in mice, inheritance of, **296**, 315
WILLIAMS, J. W., 569
Williams Seed Company, 433
WILSON, G. S., 205, 213
WILSON, M. O., 562
WILSON, P. T., **560**, 563, 564
WINGE, Ö., 452
WINKLEMAN, E., 637
Wisconsin, University of (See University)
WOODWORTH, C. M., 296
WRIGHT, S., 203, 220, 385, **603**

X-ray, 7, 18, 22–25, 28, 38, 54, 56, 58, 137, 149, 370, 371, 375, 386, 387, 434, 637, 638, 657, **674**

YAMPOLSKY, C., 434, 436, 439, 452, 453
YARNELL, S. H., 182, 185, 201, 235, 238, 253, 255, 256, 262, 265, 672
YERKES, R. M., 297, 315

Zea-Euchlaena hybrids, 481
  Chiasma formation, 493, 495, **496**
  Chromosome association, **481**, **488**, **493**, 495, **496–498**
    Diakinesis and metaphase, 488
    Pachytene, 487
    Post-diplotene, **493–495**, **496**, 500
    Relation of crossing over to, 481
  Chromosome disjunction, **493**, 495, **498**
  Chromosomes, end association of, 496
  Conjugation, 493. 495
  Crossing over, **481**, 486, 487, **492**, 493, **495–497**, 498, 500
    Cause of reduction in, 492
    Genetic studies of, 485
  Cytology, 486
  Hetero-fertilization, 486
  Sterility, pollen 492
  Translocation, 496, 499
Zea mays (See maize), 545, 695
Zeiss compound ocular, 650
ZELENY, C., 369

GENETICS

A PERIODICAL RECORD OF INVESTIGATIONS
BEARING ON HEREDITY AND
VARIATION

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TABLE OF CONTENTS

JANUARY NUMBER

(Issued January 2, 1932)

PAGE

Portrait of KARL PEARSON ..... Frontispiece

WHITING, P. W., Mutants in Habrobracon 1

CHARLES, D. R., A graph for standard errors of ratios 31

PATTERSON, J. T., A new type of mottled-eyed Drosophila due to an unstable translocation 38

MOHR, O. L., Genetical and cytological proof of somatic elimination of the fourth chromosome in *Drosophila melanogaster* 60

GRAUBARD, M. A., Inversion in *Drosophila melanogaster* 81

MARCH NUMBER

(Issued March 1, 1932)

FISHER, R. A., IMMER, F. R., and TEDIN, O., The genetical interpretation of statistics of the third degree in the study of quantitative inheritance 107

POOLE, C. F., Pollen grain studies as an indication of fertility in hybrids 125

REDFIELD, H., A comparison of triploid and diploid crossing over for chromosome II of *Drosophila melanogaster* 137

BIDDLE, R. L., The bristles of hybrids between *Drosophila melanogaster* and *Drosophila simulans* 153

EAST, E. M., Studies on self-sterility. IX. The behavior of crosses between self-sterile and self-fertile plants 175

SCHOTT, R. G., The inheritance of resistance to *Salmonella aertrycke* in various strains of mice 203

TABLE OF CONTENTS
(CONTINUED)

MAY NUMBER

(Issued May 2, 1932)

RILEY, H. P., Self-sterility in Shepherd's Purse 231
DAWSON, W. M., Inheritance of wildness and tameness in mice 296
EAST, E. M., Further observations on *Lythrum salicaria* 327
WIENER, A. S., Method of measuring linkage in human genetics; with special reference to blood groups 335
LINDSTROM, E. W., First-chromosome genes in the tomato 351
SPRAGUE, G. F., The nature and extent of hetero-fertilization in maize 358

JULY NUMBER

(Issued July 6, 1932)

DOBZHANSKY, T., The baroid mutation in *Drosophila melanogaster* ... 369
EMERSON, S., and STURTEVANT, A. H., The linkage relations of certain genes in Oenothera 393
BEADLE, G. W., Genes in maize for pollen sterility 413
FLORY, JR., W. S., Genetic and cytological investigations on *Asparagus officinalis* L. 432
CLOUDMAN, A. M., A genetic analysis of dissimilar carcinomata from the same gland of an individual mouse 468
BEADLE, G. W., The relation of crossing over to chromosome association in Zea-Euchlaena hybrids 481

TABLE OF CONTENTS

(CONTINUED)

SEPTEMBER NUMBER

(Issued September 1, 1932)

EMERSON, R. A., and ANDERSON, E. G., The A series of allelomorphs in relation to pigmentation in maize 503

SINGLETON, W. R., Cytogenetic behavior of fertile tetraploid hybrids of *Nicotiana rustica* and *Nicotiana paniculata* 510

LESLEY, J. W., Trisomic types of the tomato and their relation to the genes 545

WILSON, P. T., and JONES, H. E., Left-handedness in twins 560

CLELAND, R. E., Further data bearing upon circle-formation in Oenothera, its cause and its genetical effect 572

WRIGHT, S., General, group and special size factors 603

NOVEMBER NUMBER

(Issued November 1, 1932)

MCCRAY, F. A., Compatibility of certain Nicotiana species 621

VAN ATTA, E. A., Genetic and cytological studies on X-radiation induced dominant eye colors of Drosophila 637

MCCRAY, F. A., A partially fertile triple species hybrid in Nicotiana 660

LITTLE, C. C., and MCPHETERS, B. W., Further studies on the genetics of abnormalities appearing in the descendants of X-rayed mice 674

LAMMERTS, W. E., Inheritance of monosomics in *Nicotiana rustica* ... 689

INDEX 697

CORRIGENDA

Volume 16, 1931

Page 540, table 3, line 4, for "*ba-EE*" read "*ba-Ee*."
Page 674, table 10, last column, line 2, for "0.11" read "0.01."

Volume 17, 1932

Page 66, line 7, for "p. 64" read "p. 69."
Page 68, line 8 from bottom, for "p. 67" read "p. 75."
Page 69, line 10 from bottom, for "p. 68" read "p. 78."
Page 76, line 16, for "p. 64" read "p. 72."
Page 113, line 8 from bottom, for "$S(x-\bar{x})\ (y-\bar{y})/n-1$" read "$S(x-\bar{x})\ (y-\bar{y})/(n-1)$."

KARL PEARSON

(FRONTISPIECE)

KARL PEARSON, M.A. (Cantab.), LL.D. (St. Andrews), F.R.S., first Galton Professor of National Eugenics, Director of the Biometric Laboratory and the Francis Galton Eugenics Laboratory in the UNIVERSITY OF LONDON, was born in London, March 27, 1857, of Yorkshire parents coming of Quaker stock. His father was WILLIAM PEARSON, Queen's Council, and KARL was educated to follow his father's footsteps in a career in Law. His early schooling was secured at UNIVERSITY COLLEGE SCHOOL and by private tuition until he entered CAMBRIDGE UNIVERSITY in 1875 where he was first Scholar, then Fellow and later Honorary Fellow. He graduated Third Wrangler in 1879. After his graduation he studied under QUINCKE and KUNO FISCHER at Heidelberg and attended lectures by DU BOIS RAYMOND and BRUNS in Berlin. Returning to England he passed his examinations and was admitted to the Bar (Inner Temple) in 1882.

During 1880 to 1882 he lectured for the University Extension on science and German history, and at working-men's clubs on KARL MARX and LASSALLE. He edited and completed *The Common Sense of the Exact Sciences*, by W. K. CLIFFORD, and *The History of the Theory of Elasticity*, by ISAAC TODHUNTER.

Owing to the illness of a friend he was induced to lecture on Mathematics in a London college and was so successful in this work that he abandoned the law for a career in mathematics and science. He published a number of papers on applied mathematics, and finally was appointed Professor of the subject in 1884 at UNIVERSITY COLLEGE, London, a position he held until 1911.

His friendship with WELDON and GALTON, from 1888 on, led him to the mathematical theory of statistics, especially in relation to living forms. He gave the first course of lectures on applied statistics in 1890, and invented the term "Biometry" for the application of the newer statistical methods to problems concerning plants and animals, and the Biometrical Laboratory was started in the early nineties.

Biometrika was started in 1901 in conjunction with WELDON and GALTON and has continued under PEARSON'S editorship to the present time, being now in its twenty-fourth volume. In 1906 GALTON'S Eugenics Record Office of 1904 was remodeled by PEARSON as the Eugenics Laboratory and was supported financially and morally by GALTON till his death in 1911.

In that year PEARSON gave up his mathematical chair, and was elected at the UNIVERSITY OF LONDON, first Galton Professor of National Eugenics. The publications of the Biometric and Eugenics Laboratories have appeared continuously since their respective foundations. In 1925 the Eugenics Laboratory began a new journal, *The Annals of Eugenics*, which is now in its fourth volume.

Among PEARSON'S more notable books have been *The Ethic of Free Thought* (1887, 1901), *Chances of Death and Other Studies in Evolution* (1897), *Grammar of Science* (1899, 1900, 1911), *National Life from the Standpoint of Science* (1901), *Tables for Statisticians* (1914, 1924, 1930), *Life, Letters, and Labours of Francis Galton* (1915–1930). The last is much more than an ordinary biography, containing a critical account of the content of every paper written by

GALTON. It contains a detailed account of the birth of Biometry and Eugenics, and a full acknowledgment of the inspiration which PEARSON drew from GALTON.

PEARSON was elected a Fellow of the Royal Society in 1896, and later received from the same Society the Darwin Medal for his numerous contributions to the mathematical theory of evolution and heredity. He is an Honorary or Corresponding Member of many scientific societies and academies, including the AMERICAN STATISTICAL SOCIETY, the ANTHROPOLOGICAL SOCIETY OF WASHINGTON and the NATIONAL ACADEMY OF SCIENCES.

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GENETICS, NOVEMBER, 1932

TABLE OF CONTENTS

	PAGE
McCRAY, F. A., Compatibility of certain Nicotiana species	621
VAN ATTA, E. A., Genetic and cytological studies on X-radiation induced dominant eye colors of Drosophila	637
McCRAY, F. A., A partially fertile triple species hybrid in Nicotiana	660
LITTLE, C. C., AND McPHETERS, B. W., Further studies on the genetics of abnormalities appearing in the descendants of X-rayed mice	674
LAMMERTS, W. E., Inheritance of monosomics in *Nicotiana rustica*	689

VI INTERNATIONAL BOTANICAL CONGRESS

According to a decision by the V INTERNATIONAL BOTANICAL CONGRESS at Cambridge in 1930, the SIXTH CONGRESS will be held in Holland in 1935. An Executive Committee has been formed, the President of which is Professor Doctor F. A. F. C. WENT (Utrecht), while Professor Doctor J. C. SCHOUTE (Groningen) will act as Vice-President, Doctor W. C. DE LEEUW (Bilthoven) as Treasurer and Doctor M. J. SIRKS (Wageningen) as Secretary. The Committee has decided that the VI CONGRESS will meet at Amsterdam, September 9–14, 1935. Scientific societies are kindly requested to reckon with these data in planning their own meetings.

Contents of previous issues of GENETICS can be found by consulting the AGRICULTURAL INDEX

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C 30